

A CHECKLIST OF AND ILLUSTRATED KEY TO THE  
GENERA AND SPECIES OF THE CENTRAL AND  
NORTH AMERICAN CAMBARINCOLIDAE  
(CLITELLATA: BRANCHIOBDELLIDA)

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*Abstract.* — This paper treats the 90 species of Cambarincolidae known from Central and North America. Each species is illustrated and its synonyms, taxonomic references, type specimen disposition, and distribution are given. Keys are provided to the family's nine genera and to the 48 species of *Cambarincola*, 2 species of *Ceratodrilus*, 7 species of *Ellisodrilus*, 4 species of *Oedipodrilus*, 8 species of *Pterodrilus*, and 18 species of *Sathodrilus*, *Magmatodrilus*, *Tetodrilus*, and *Triannulata* are each represented by a single species.

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The branchiobdellidans are obligate epizoites on freshwater crustaceans throughout the Holarctic region except, apparently, in Central Asia between the Ural Mountains and the Amur drainage (Holt 1968a). The greatest diversity of families and species is found in North America. This may be an artifact of collecting, as we have less information from other regions except Europe where only a few species are found. In Asia only Yamaguchi has done any significant work on the Japanese and Korean faunas. Despite the greater body of work on the North American branchiobdellidans, it is likely that only a small fraction of this fauna has been accorded taxonomic treatment. Most genera and species of North American branchiobdellidans are assigned to the family Cambarincolidae (Holt 1986). The phylogenetic position and classification of the Branchiobdellida is discussed by Gelder & Brinkhurst (1990), Holt (1986, 1989a), and Sawyer (1986).

#### Methods

Types or topotypes of all taxa of the cambarincolids have been studied in Holt's laboratory and detailed methods for preserving

and studying specimens are found in Holt (1986). Additional methods include Gelder & Hall's (1990) use of a mixture of clove oil and methyl salicylate (oil of wintergreen), as branchiobdellidans, particularly gill-inhabiting forms, are often twisted and distorted when methyl salicylate alone is used in the preparation of entire animals. The use of Nomarski differential interference contrast optics gives a much clearer view of internal structures in whole animals than does bright field illumination. When time and the availability of specimens permit, the worms should be relaxed with an appropriate agent, such as chloral hydrate and, after fixation in alcohol-formalin, lightly stained. For field collection, alcohol-formalin (Holt 1963) still seems the best and easiest preservative to use.

All of the branchiobdellidan material, including types, studied by Holt and their accompanying field notes have been deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. These specimens are identified by the accession numbers (USNM) of the National Museum, or by Holt's accession numbers (PCH . . .). A few paratypes are in the collection of the

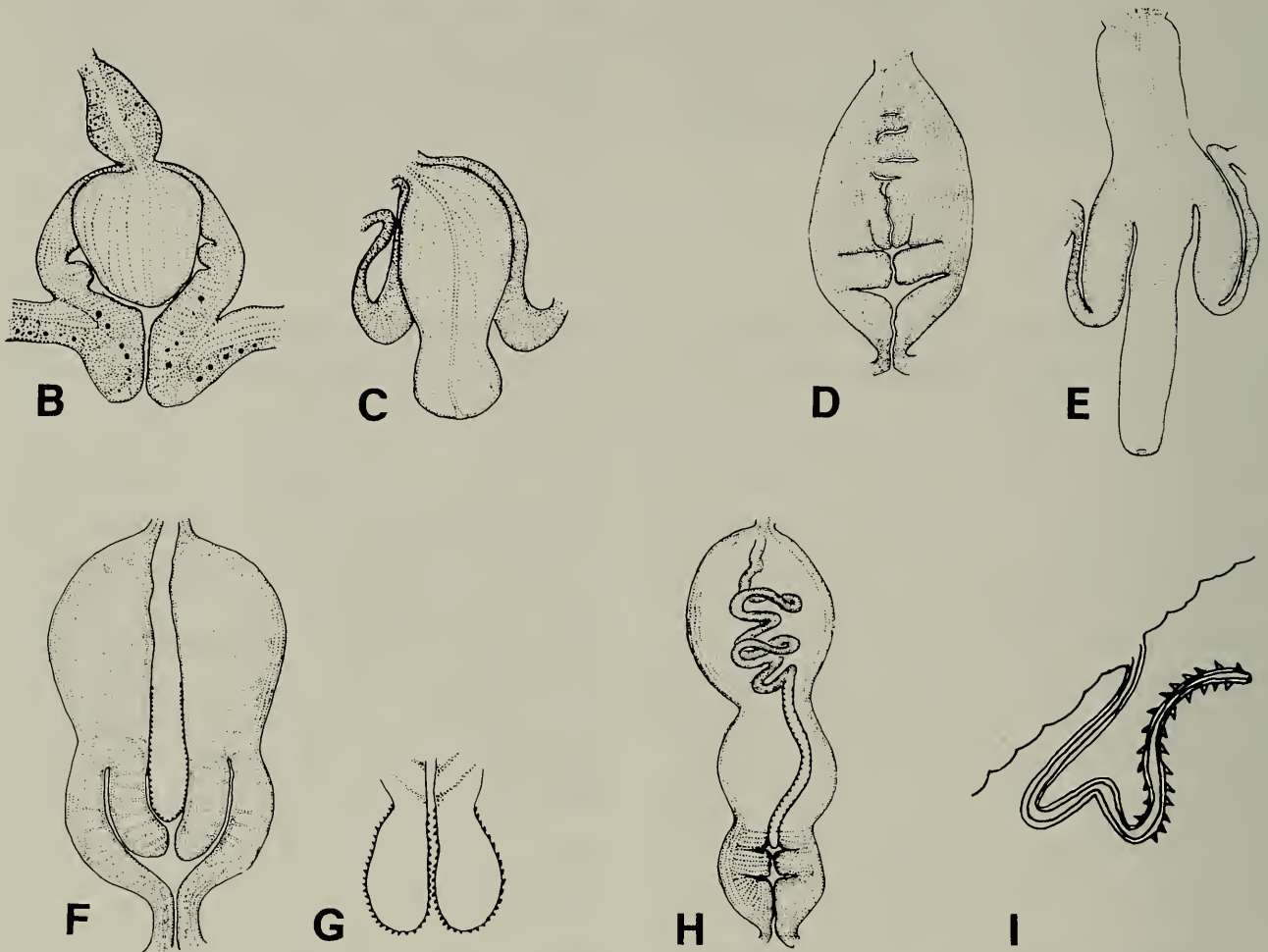
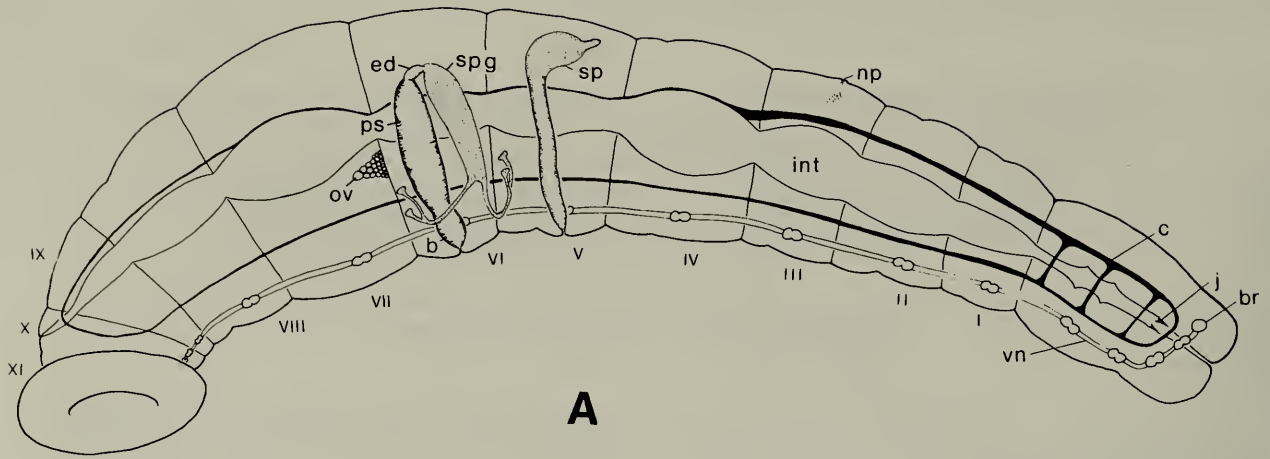


Fig. 1. A, generalized branchiobdellidan in lateral view; Abbreviations as follows: I–XI, Trunk Segments; B, Bursa; BR, Brain; C, Circulatory System; DR, Dorsal Ridge; DRP, Digital Projections of the Dorsal Ridge; EBP, Ental Bulb of Prostate; ELS, Ental Lobe of the Seminiducal Gland; EPS, Ental Process of Spermatheca; ED, Ejaculatory Duct; EP, Everted Penis; FVE, Funnel of Vas Deferens; HDP, Histologically Differentiated Prostate; INT, Intestine; IPR, Incompletely Separated Prostate; J, Jaws; NP, Nephridiopore; OV, Ovary; PR, Prostate; PS, Penial Sheath; PT, Peristomal Tentacles; PP, Prostatic Protuberance; PB, Prostate Bulb; RP, Retracted Penis; SPG, Seminiducal Gland; SB, Bulb of Spermatheca; SD, Spermathecal Duct; SMR, Supernumerary Muscles of Dorsal Ridge; VN, Ventral Nerve Cord; VD, Vas Deferens (from Holt 1969, 1986); B–C, eversible penis of *Pterodrilus alcicornis*; B, withdrawn; C, everted; D–E, eversible penis of *Cambarincola pamelaie*; D, withdrawn; E, everted; F–G, protrusible penis of *Oedipodrilus oedipus*; F, withdrawn; G, protruded, H, withdrawn protrusible penis of *Oedipodrilus cuetzalanae*; I, protruded protrusible penis of *Oedipodrilus macbaini*. Unless otherwise noted, the figures of each species on the following plates are arranged, from left to right, as follows: lateral view of whole specimen, lateral view of reproductive system, ventral view of upper jaw (top) and dorsal view of lower jaw (bottom); and lateral views of upper jaw (top) and lower jaw (bottom). Abbreviations are given above.

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The characters used in the taxonomy of the branchiobdellidans (Fig. 1A) have changed over the years with the recognition that structures once thought to be common to all members of the class are not so and the discovery of previously unrecognized features. Summaries, in each case incomplete, may be found in Yamaguchi (1934), Goodnight (1940), Holt (1953, 1960a, 1960b), Hoffman (1963), and Gelder & Brinkhurst (1990). An example of this is the use by Gelder & Hall (1990) of the number of oral papillae to separate species. Previously these putative sensory structures were, at best, simply noted as present or absent. Further studies should be done to confirm the taxonomic usefulness of these papillae.

In the preparation of this paper all figures were either redrawn from the originals or from enlarged illustrations in the literature in order to achieve uniformity of style. The correctly constructed term "semniducal gland" replaces "spermiducal gland" in the taxonomic keys. This paper cites primarily taxonomic papers and its literature cited is, therefore, not intended to be a complete bibliography of the branchiobdellidans. The species names of all crayfish host records have been updated according to Hobbs (1989). As the literature citations for these names are provided by Hobbs, they are not repeated in this paper. Unless otherwise noted, all hosts are crayfish.

*Nomen inquirendum.* — *Cambarincola okadai* Yamaguchi, 1933. This nominal species was described from a specimen introduced with its American host into Lake Chuzenji, Nikko, Japan. Unfortunately, the location of the type(s) is unknown and the description could apply to any one of several American species.

#### The Checklist

##### *Cambarincola* Ellis, 1912

*Cambarincola* Ellis, 1912:481.

*Type species.* — *Cambarincola macrodonta* Ellis, 1912, by original designation.

*Gender.* — Masculine.

*Cambarincola acudentatus* Holt, 1973  
Figs. 2–5

*Cambarincola acudentatus* Holt, 1973b:11–13.

*Types.* — Holotype and 1 paratype, USNM 45435, 6 paratypes, PCH 489, 4 paratypes, IBUM, on the isopods *Speocirolana bolivari* and *S. pelaezi*, from Grutas de Quintero. 11 km SW of Ciudad Monte, Tanaulipas, México, 14 May 1950, by Alejandro Villalobos.

*Distribution.* — Known only from the type locality.

*Cambarincola alienus* Holt, 1963  
Figs. 6–10

*Cambarincola aliena* Holt, 1963:97–100.  
*Cambarincola alienus.* — Holt, 1973c:10.

*Types.* — Holotype, USNM 30415, 7 paratypes, USNM 30416, 7 paratypes, PCH 1325, on the isopod *Asellus alabamensis* (Stafford), from Wet Cave, Franklin Co., Tennessee, by T. C. Barr [date lost].

*Distribution.* — Known only from the type locality.

Notes: *Cambarincola steevesi* Holt, 1973c, may be conspecific with or a local race of *C. aliena*.

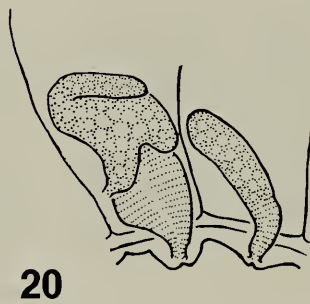
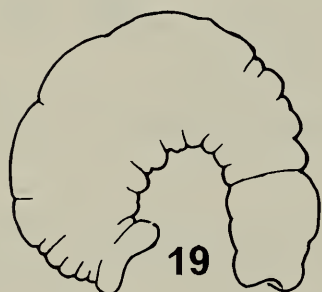
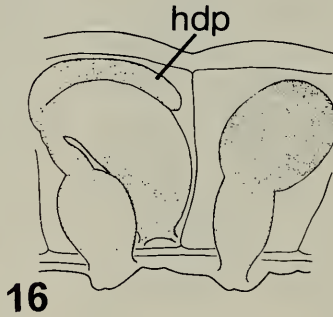
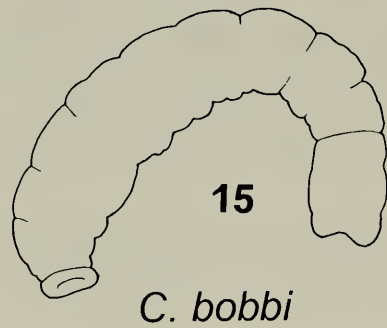
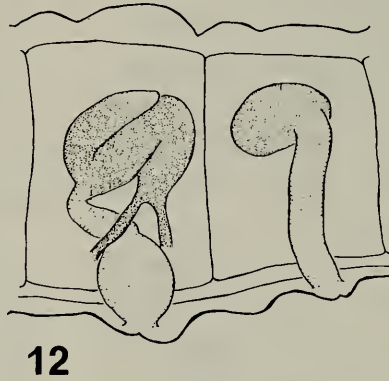
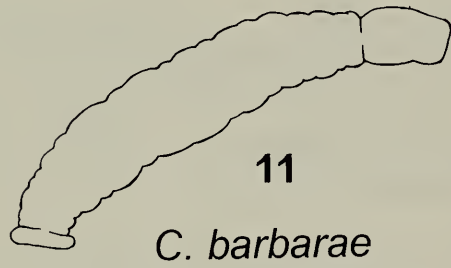
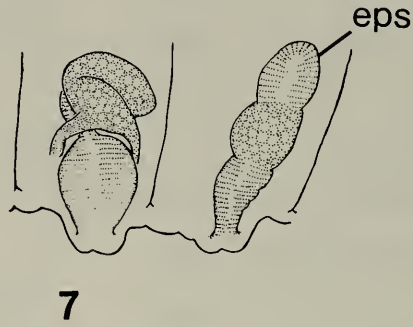
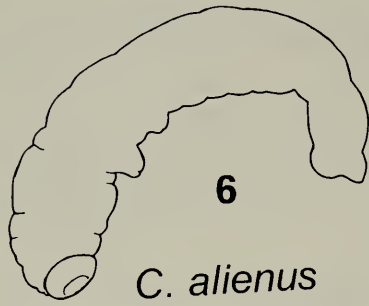
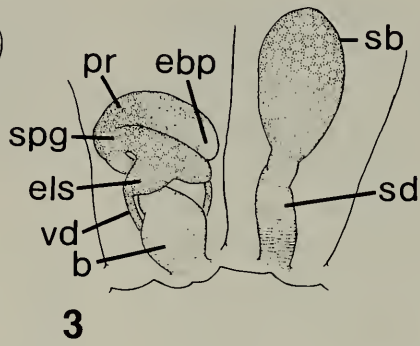
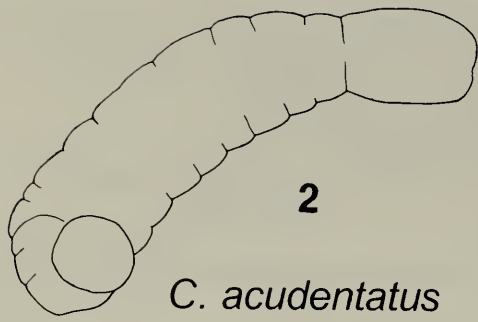
*Cambarincola barbarae* Holt, 1981  
Figs. 11–14

*Cambarincola barbarae* Holt, 1981a:677–679.

*Types.* — Holotype, USNM 54639, 5 paratypes, PCH 1101, on *Procambarus* (*Scapulicambarus*) *clarkii* (Girard), from irrigation ditch 3.1 mi E of Salvang, Santa Barbara Co., California, by Perry C. and Virgie F. Holt, 3 Jul 1960.

*Distribution.* — Santa Barbara and Sonoma Counties, California.

Notes: "*Cambarincola barbarae* occurs



Figs. 2-22. 2-5, *Cambarincola acudentatus* Holt, 2, ventro-lateral view; 6-10, *Cambarincola alienus* Holt; 11-14, *Cambarincola barbarae* Holt; 15-18, *Cambarincola bobbi* Holt; 19-22, *Cambarincola branchiophilus* Holt.

upon an introduced species (Hobbs, 1972: 72) which also serves as a host for *C. mesochoreus* Hoffman, 1963, and *C. fallax* Hoffman, 1963. The former species is widespread in the Mississippi Valley and the latter in the Appalachians and were possibly introduced with their host. This may be so for *C. barbarae*" (Holt 1981a:679).

*Cambarincola bobbi* Holt, 1988

Figs. 15–18

*Cambarincola bobbi* Holt, 1988b:794–808.

*Types.* — Holotype, USNM 101496, 4 paratypes, USNM 101497–101499, on *Cambarus bartonii bartonii* (Fabricius), from a medium-sized stream in Tom's Brook (a town) 5.7 mi S of Strasburg, Shenandoah Co., Virginia, by Marvin L. Bobb and Perry C. Holt, 22 Jul 1948.

*Distribution.* — Known only from the type locality.

*Cambarincola branchiophilus* Holt, 1954

Figs. 19–22

*Cambarincola branchiophila* Holt, 1954: 168–172. — Hoffman, 1963:317–319.

*Cambarincola branchiophilus.* — Holt, 1973b:10.

*Types.* — Holotype, USNM 25855, 6 paratypes, PCH 407 USNM, on *Cambarus bartonii bartonii* (Fabricius), and *C. sciotosensis* Rhoades, from Sinking Creek at crossing of State Highway 700, Giles Co., Virginia, by Frank D. Kiser, Cornelia Tuten and Perry C. Holt, 3 Jul 1950.

*Distribution.* — Known only from the type locality.

*Cambarincola carcinophilus* Holt, 1973

Figs. 23–28

*Cambarincola carcinophilus* Holt, 1973b: 13–14.

*Types.* — Holotype, USNM 45439, 1 paratype, IBUM, 1 paratype, PCH 698, on

the freshwater crab *Pseudothelophusa veracruzana*, from Rio Tapalapa, Santiago, Tuxtla, México, by Alejandro Villalobos and Horton H. Hobbs, Jr., 1957.

*Distribution.* — Two locations in the lowlands of Southern Veracruz.

*Notes:* The specimens taken in 1957 by Villalobos and Hobbs from the Arroyo de Zapoapan de Cabaña were associated with not only the crab *P. veracruzana*, but also with the crayfish *Procambarus zapoapensis* Villalobos.

*Cambarincola chirocephala* Ellis, 1919

Figs. 29–34

*Cambarincola chirocephala* Ellis, 1919:263–264. — Goodnight, 1940:37–38. — Holt & Hoffman, 1959:103. — Hoffman, 1963: 348–351.

*Cambarincola chirocephalus.* — Holt, 1973b:9 [unjustified emendation].

*Types.* — Holotype, USNM 17713, on *Orconectes virilis* Hagen, from Rolla, Phelps Co., Missouri, by J. Barley, date unknown.

*Distribution.* — From western Tennessee north to Indiana, westward to Oklahoma and Kansas.

*Notes:* *Cambarincola chirocephala* appears to intergrade with *C. philadelphicus* in western Tennessee (Hoffman 1963:345).

*Cambarincola demissus* Hoffman, 1963

Figs. 35–36

*Cambarincola demissa* Hoffman, 1963:365–367.

*Cambarincola demissus.* — Holt, 1973b:10.

*Types.* — Holotype and 4 paratypes, USNM 29948, on *Orconectes erichsonianus* Faxon, and *O. rusticus* (Girard), from the Powell River at Big Stone Gap, Wise Co., Virginia, by H. H. Hobbs, Jr. and C. W. Hart, Jr., 17 Jun 1950.

*Distribution.* — Mountain regions of southwestern Virginia.

*Cambarincola dubius* Holt, 1973

Figs. 37–42

*Cambarincola dubius* Holt, 1973c:234–236.

*Types.* — Holotype, USNM 49673, 2 paratypes, USNM 49674, 4 paratypes, PCH 2763, on *Cambarus laevis* Faxon, and *Orconectes inermis testii* (Hay), from May's Cave, Monroe Co., Indiana, by Horton H. Hobbs, III, 20 Sep 1969.

*Distribution.* — Caves in Monroe Co., Indiana.

*Cambarincola ellisi* Holt, 1973

Figs. 43–48

*Cambarincola ellisi* Holt, 1973b:14–16.

*Types.* — Holotype, USNM 45433, on *Procambarus regiomontanus* Villalobos, from Rio San Juan, San Juan, Nuevo Leon, Mexico, by Salvador Contreras, 18 Apr 1964. One paratype, PCH 1844, on *P. regiomontanus*, from Arroyo de la Cruz, km 245 de la carretera Ciudad México-Monterey, by A. Villalobos, 14 Feb 1964.

*Distribution.* — Known only from the type locality.

*Notes:* *Cambarincola ellisi* is known from a tributary on the Rio Grande (Rio Bravo) and is geographically nearer the branchiobdellidans of the United States than of Mexico.

*Cambarincola fallax* Hoffman, 1963

Figs. 49–54

*Cambarincola fallax* Hoffman, 1963:256–259.—Hobbs et al., 1967:54–55.—Holt, 1969:207; 1973c:238; 1981a:679–680.

*Types.* — Holotype and 4 paratypes, USNM 29945, additional paratypes, PCH 904, on "*Cambarus longulus* subsp." [either *C. longirostris* Faxon, or *C. longulus* Girard], from Maiden Spring Creek, Tazewell Co., Virginia, by Richard L. Hoffman, 19 Jun 1959.

*Distribution.* — Appalachian Mountains from Canada to Georgia; one specimen from

Sonoma Co., California. In the southern parts of its range this species is confined to higher elevations.

*Notes:* The specimen from California represents either an introduction, or less likely a new, but closely related species.

*Cambarincola floridanus* Goodnight, 1941

Figs. 55–60

*Cambarincola floridanus* Goodnight, 1941:73–74.—Hoffman, 1963:368.—Holt, 1973a:90–93.

*Types.* — Holotype, USNM 20570, on *Procambarus fallax* (Hagen), collected 6.8 mi S of Lamont, Taylor Co., Florida, by Horton H. Hobbs, Jr., 18 Mar 1939.

*Distribution.* — The type locality and one locality in Liberty Co., Florida.

*Notes:* In the paragraph beginning "The spermiducal gland . . ." (Holt 1973a:92) a *lapsus* resulted in "ectally" being written instead of the obviously correct "entally."

*Cambarincola goodnighti* Holt, 1973

Figs. 61–66

*Cambarincola goodnighti* Holt, 1973a:88–90.

*Types.* — Holotype, USNM 49706, 1 paratype, USNM 48707, 1 paratype, PCH 2607, on *Procambarus fallax* (Hagen), and *P. paeninsulanus* (Faxon), collected 5 mi N of St. Augustine, St. Johns Co., Florida (Collector and date unknown).

*Distribution.* — Known only from the type locality.

*Cambarincola gracilis* Robinson, 1954

Figs. 67–70

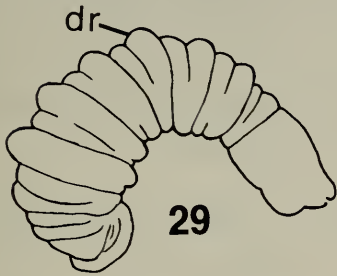
*Cambarincola gracilis* Robinson, 1954:467–468.—Holt & Hoffman, 1959:97–103.—Hoffman, 1963:369.—Holt, 1981a:680–685.—Gelder & Hall, 1990:2354.

*Types.* — Holotype and 10 paratypes, USNM 26110, on *Pacifastacus leniusculus kalamathensis* (Stimpson), from creek on



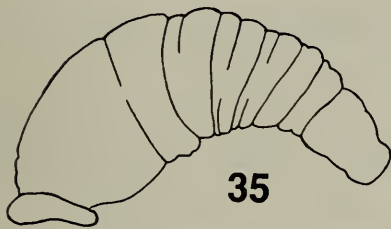
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*C. carcinophilus*



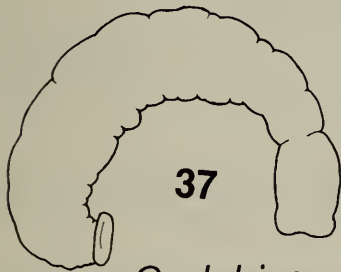
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*C. chirocephala*



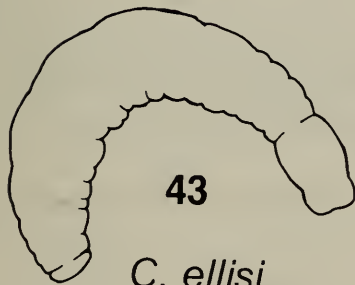
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*C. demissus*



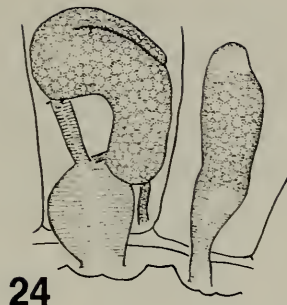
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*C. dubius*

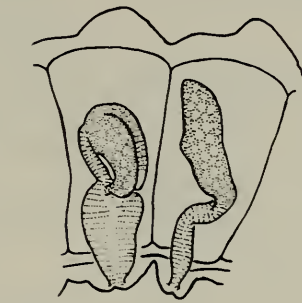


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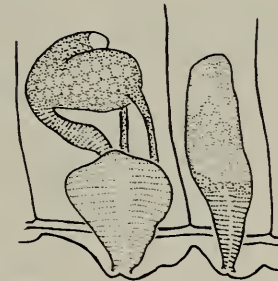
*C. ellisi*



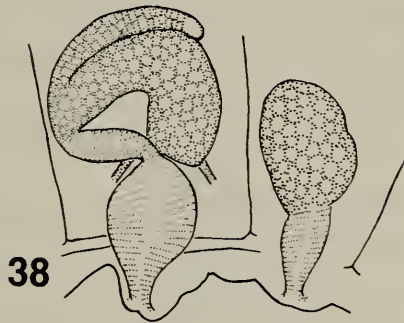
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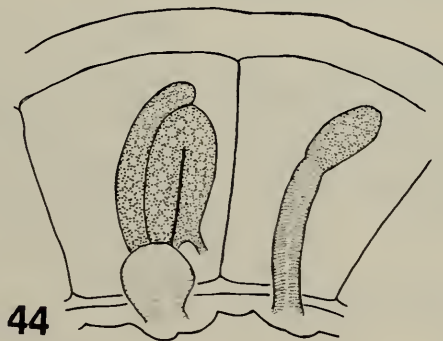
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Figs. 23-48. 23-28, *Cambarincola carcinophilus* Holt; 29-34, *Cambarincola chirocephala* Ellis; 35-36, *Cambarincola demissus* Hoffman; 37-42, *Cambarincola dubius* Holt; 43-48, *Cambarincola ellisi* Holt.

campus of Whitman College, Walla Walla, Walla Walla Co., Washington, by A. G. Rempel, 11 Aug 1952; 2 paratypes, USNM 26111, on *P. l. klamathensis*, from Klamath River, 1 mi W of Ash Creek, Siskiyou Co., California, by Harold Wolf, 27 Oct 1952; 1 paratype, USNM 26112, on *P. l. trowbridgii* (Stimpson), from Burdette Creek, Burnaby, British Columbia, by G. Clifford Carl, 21 May 1942.

*Distribution.*—From southern California to southern British Columbia in streams of the Pacific versant.

*Notes:* Holt's statement (Holt 1981a:682) that the prostate is subequal in length and diameter to the spermiducal gland is an inexplicable error (see Holt 1981a:681, fig. 2). *Cambarincola gracilis* is the second most common species of branchiobdellidan in collections from the Pacific drainage in the United States and Canada.

*Cambarincola heterognathus* Hoffman, 1963  
Figs. 71–76

*Cambarincola heterognatha* Hoffman, 1963: 362–365.

*Cambarincola heterognathus.*—Holt, 1973a: 95; 1973b:10.

*Types.*—Holotype and 1 paratype, USNM 29947, on *Cambarus* sp., from a tributary to Big Wilson Creek, 4 mi N of Mouth of Wilson, on State Highway 16, Grayson Co., Virginia, by Horton H. Hobbs, Jr., and C. W. Hart, 14 Jun 1950.

*Distribution.*—From northwestern Virginia and adjacent West Virginia south and west to the central eastern parts of Kentucky and Tennessee; disjunct populations in Leon and Calhoun Counties, Florida.

*Cambarincola hoffmani* Holt, 1973  
Figs. 77–82

*Cambarincola hoffmani* Holt, 1973b:16–17.

*Types.*—Holotype, USNM 45447, on *Procambarus hoffmanni* (Villalobos), from

Arroyo de Tlatentilojan, at Los Estajos, 6 km NE of Zihuateutla, Puebla, México, by Alejandro Villalobos, 11 Nov 1949; 2 paratypes, PCH 1622, on *Procambarus caballeroi* Villalobos, from Villa Juárez, Puebla, México, by Alejandro Villalobos, May 1944.

*Distribution.*—Known only from the type locality.

*Notes:* *Cambarincola hoffmani* may be an inhabitant of the gill chambers of its hosts (Holt 1973b:17). The spelling is correct, as the species was named from R. L. Hoffman, not for the host crayfish.

*Cambarincola holostoma* Hoffman, 1963  
Figs. 83–87

*Cambarincola holostoma* Hoffman, 1963: 359–361.

*Cambarincola holostomus.*—Holt, 1973b:10 [unjustified emendation].

*Types.*—Holotype and 4 paratypes, USNM 29946, 2 paratypes, PCH 599, on “*Cambarus bartonii*” [probably *C. b. cavatus* Hay] and *C. longulus* Girard, from Crab Run, Highland Co., Virginia, by L. B. Holthuis, 25 Oct 1952.

*Distribution.*—Western Virginia in the headwaters of the Potomac and James Rivers (Hobbs et al. 1967:57).

*Cambarincola holti* Hoffman, 1963  
Figs. 88–89

*Cambarincola holti* Hoffman, 1963:314–316.

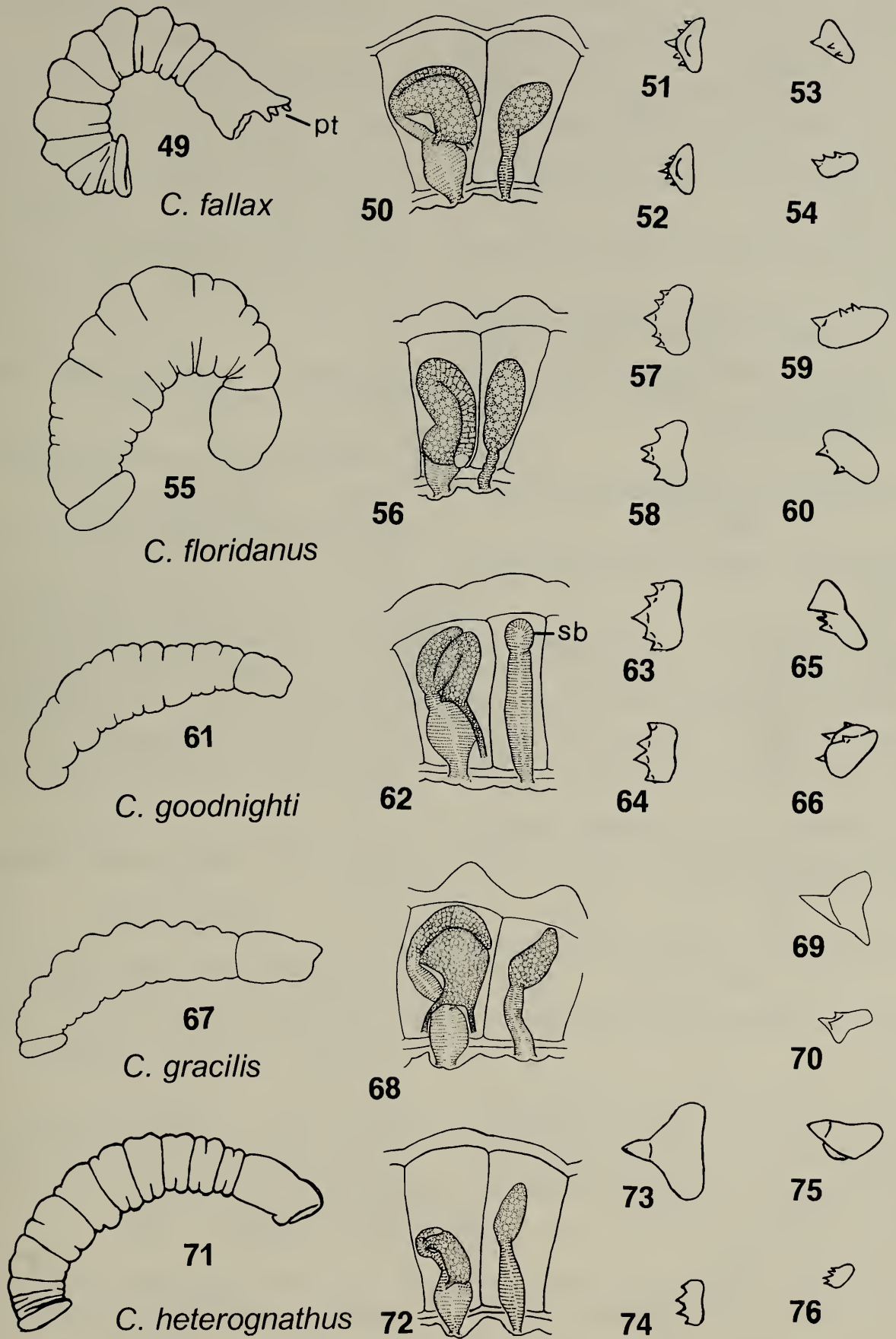
*Types.*—Holotype and paratypes, USNM 29940, on *Cambarus* sp., from a stream in the southern part of Somerset, Pulaski Co., Kentucky, by Perry C. and Virgie F. Holt, 28 Jul 1958.

*Distribution.*—Known only from the type locality.

*Cambarincola illinoisensis* Holt, 1982  
Figs. 90–93

*Cambarincola illinoisensis* Holt, 1982:251–255.





Figs. 49-76. 49-54, *Cambarincola fallax* Hoffman; 55-60, *Cambarincola floridanus* Goodnight; 61-66, *Cambarincola goodnighti* Holt; 67-70, *Cambarincola gracilis* Robinson; 71-76, *Cambarincola heterognathus* Hoffman.

*Types.* — Holotype, USNM 65225, 3 paratypes, USNM 65226, 5 paratypes, PCH 840, on *Orconectes virilis* Hagen, from a prairie stream (possibly one of the two Sugar or two Mud Creeks that drain into the Iroquois River) N of Stockland, Iroquois Co., Illinois, by Perry C. and Virgie F. Holt, 25 Jul 1958.

*Distribution.* — Known only from the type locality.

Notes: The protruded penes of *C. illinoisensis* are similar in some respects to those of species of *Sathodrilus*, but there are not enough data now to unite these genera (see Holt 1982:254–255).

*Cambarincola ingens* Hoffman, 1963  
Figs. 94–97

*Cambarincola ingens* Hoffman, 1963:333–336.

*Types.* — Holotype and 2 paratypes, USNM 29944, on *Cambarus sciotensis* Rhoades, from Sinking Creek, Giles Co., Virginia, by Ben I. Johns, 27 Jun 1953. Topotypes, taken by others, PCH 234, 407, 499.

*Distribution.* — The southern Appalachians in North Carolina, Tennessee, Virginia, and West Virginia.

*Cambarincola jamapaensis* Holt, 1973  
Figs. 98–103

*Cambarincola jamapaensis* Holt, 1973b:17–20.

*Types.* — Holotype and 5 immature paratypes, USNM 45438, 1 paratype, PCH 1592, on *Procambarus mexicanus* (Erichson), from the Rio Jamapa, 7 km NE of Coscomatepec, Veracruz, México, by Perry C. and Virgie F. Holt, 9 Jul 1962.

*Distribution.* — Known with certainty only from the type locality; specimens from two localities in Puebla, México, have tentatively been assigned to this species (Holt 1973b:20).

*Cambarincola leoni* Holt, 1973  
Figs. 104–106

*Cambarincola leoni* Holt, 1973c:226–229.

*Types.* — Holotype, USNM 49676, 1 paratype, USNM 40677, on *Procambarus orcinus* Hobbs & Means, from Gopher Sink, Leon Co., Florida, by D. Bruce Means and Joseph Halusky, 3 Apr 1971; 5 paratypes, PCH 2756, on *P. orcinus*, from Gopher Sink, by D. Bruce Means and J. F. Berry, 26 Feb 1971.

*Distribution.* — Caves in Leon, Alachua and Marion Counties, Florida.

*Cambarincola leptadenus* Holt, 1973  
Figs. 107–111

*Cambarincola leptadenus* Holt, 1973c:231–234.

*Types.* — Holotype, USNM 49678, 1 paratype, USNM 49679, 2 paratypes, PCH 2739, on *Cambarus tenebrosus* Hay, from Bethel Cave, Perry Co., Tennessee, by Horton H. Hobbs, III, 6 Oct 1968.

*Distribution.* — Known only from the type locality.

*Cambarincola macrocephala* Goodnight, 1943  
Figs. 112–116

*Cambarincola macrocephala* (inadvertent misspelling) Goodnight, 1943:100–101.

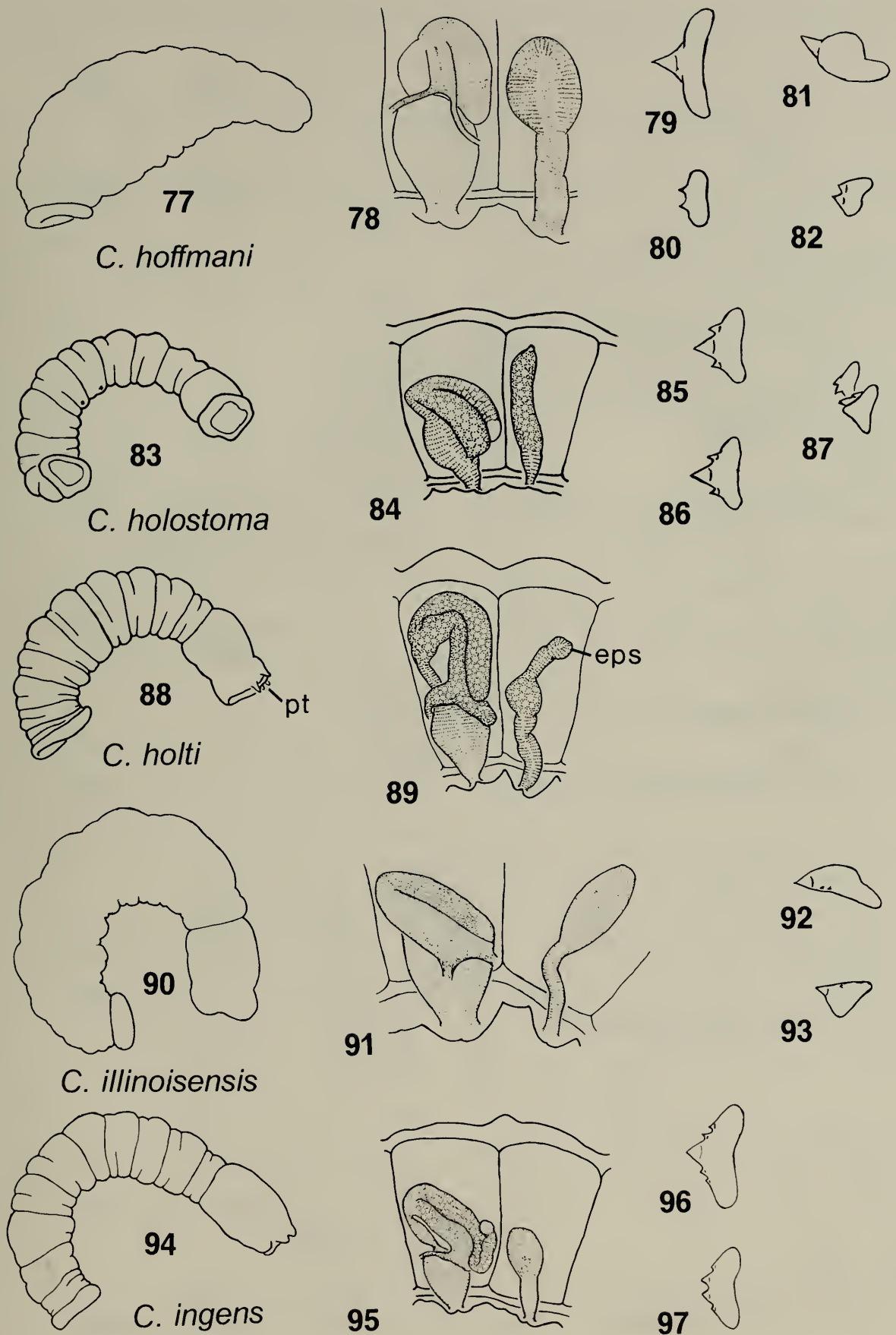
*Cambarincola macrocephala.* — Holt & Hoffman, 1959:103. — Hoffman, 1963:312–314.

*Cambarincola macrocephelus.* — Holt, 1973b:10 [unjustified emendation]; Holt, 1981a:685, fig. 3.

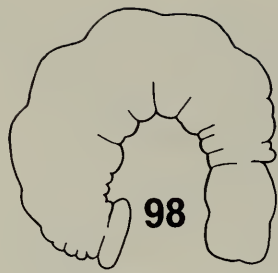
*Cambarincola macrocephalus.* — Holt, 1981a:685–689.

*Types.* — Holotype, USNM 20598, on *Pacifastacus gambelii* (Girard), from Polecat Creek, Teton Co., Wyoming, by Robert C. Brown, 16 Aug 1941.

*Distribution.* — The upper reaches of the



Figs. 77-97. 77-82, *Cambarincola hoffmani* Holt; 83-87, *Cambarincola holostoma* Hoffman; 88-89, *Cambarincola holti* Hoffman; 90-93, *Cambarincola illinoisensis* Holt; 94-97, *Cambarincola ingens* Hoffman.



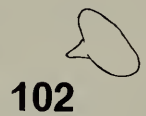
98  
*C. jamapaensis*



99



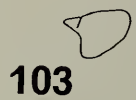
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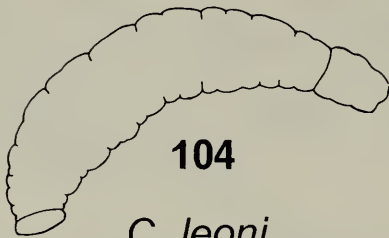
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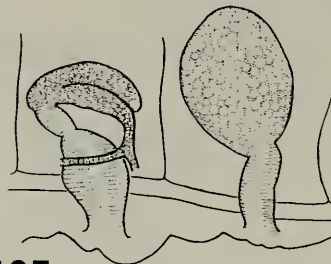
101



103



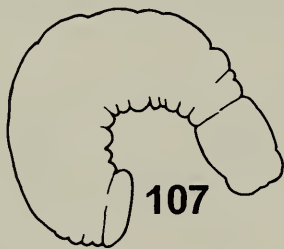
104  
*C. leoni*



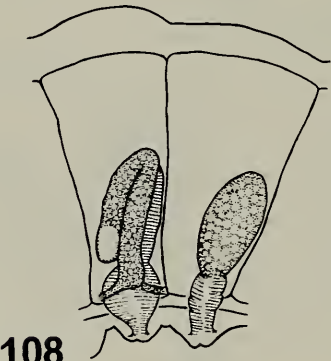
105



106



107  
*C. leptadenus*



108



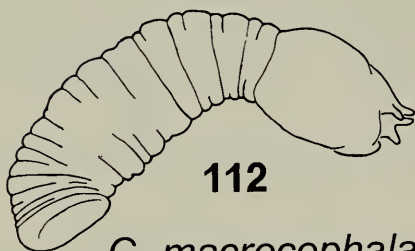
109



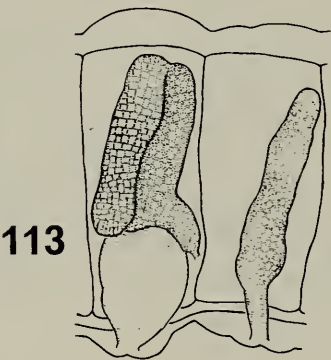
110



111



112  
*C. macrocephala*



113



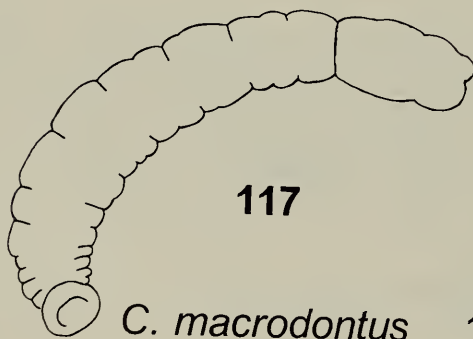
114



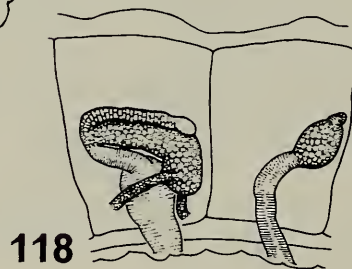
116



115



117  
*C. macrodontus*



118



119



121



120



122

Figs. 98-122. 98-103, *Cambarincola jamapaensis* Holt; 104-106, *Cambarincola leoni* Holt; 107-111, *Cambarincola leptadenus* Holt; 112-116, *Cambarincola macrocephala* Goodnight; 117-122, *Cambarincola macrodontus* Ellis.

Snake River in Idaho and Wyoming (Holt 1981a:688).

*Cambarincola macrodontus* Ellis, 1912  
Figs. 117–112

*Cambarincola macrodonta* Ellis, 1912:481–484; 1919:257.—Hall, 1914:190.—Goodnight, 1940:31.—Holt & Hoffman, 1959:97.—Hoffman, 1963:352.

*Cambarincola macrodontus*.—Holt, 1973b:9.

*Types*.—Holotype and 2 paratypes, USNM 53794, on *Cambarus diogenes* Girard, from a stream in Boulder, Boulder Co., Colorado, by Max M. Ellis, date unknown.

*Distribution*.—The high plains of the central United States, doubtfully from Las Vegas, Nevada (see Hoffman 1963:353–354).

*Cambarincola manni* Holt, 1973  
Figs. 123–128

*Cambarincola manni* Holt, 1973a:85–88.

*Types*.—Holotype, 9 paratypes, USNM 48700, on *Procambarus fallax* (Hagen), from Lake Martha, at 612 E. Lake Martha Drive, Winter Haven, Polk Co., Florida, by Chester A. Mann, 12 Jan 1964; 1 paratype, USNM 48701, on *P. fallax*, from canal between Lake Buckeye and Lake Fanny, Winter Haven, Polk Co., Florida, by Chester A. Mann and Perry C. Holt, 20 Apr 1963; 1 paratype, PCH 1670, on *P. fallax*, from Lake Martha, Winter Haven, Polk Co., Florida, by Chester A. Mann and Perry C. Holt, 20 Apr 1963; 10 paratypes, PCH 1793, from the type locality; 5 paratypes, PCH 1673, on *Procambarus paeninsulanus* (Faxon), from slough, 13 mi NW of Inglis, Levy Co., Florida, by Perry C. and Virgie F. Holt, 26 Apr 1963.

*Distribution*.—Florida peninsular.

*Notes*: *Cambarincola manni* appears to be confined to peninsular Florida and is the only branchiobdellidan from the southern portion of the state, but overlaps *C. osceolai*

in the northern part of the state (see Holt 1973a:88, fig. 1).

*Cambarincola marthae* Holt, 1973  
Figs. 129–134

*Cambarincola marthae* Holt, 1973c:221–224.

*Types*.—Holotype, USNM 49509, 1 paratype, PCH 2767, on the isopod *Asellus alabamensis* (Stafford), from Carter's Cave, Jackson Co., Tennessee, by John E. and Martha R. Cooper, 21 Sep 1968.

*Distribution*.—Known only from the type locality.

*Cambarincola mesochoreus* Hoffman, 1963  
Figs. 135–137

*Cambarincola vitrea* (in part).—Ellis, 1919:257–258.

*Cambarincola macrodonta* (in part).—Ellis, 1919:257.

*Cambarincola mesochorea* Hoffman, 1963:307–311.

*Cambarincola mesochoreus*.—Holt, 1973b:10; 1981a:689.

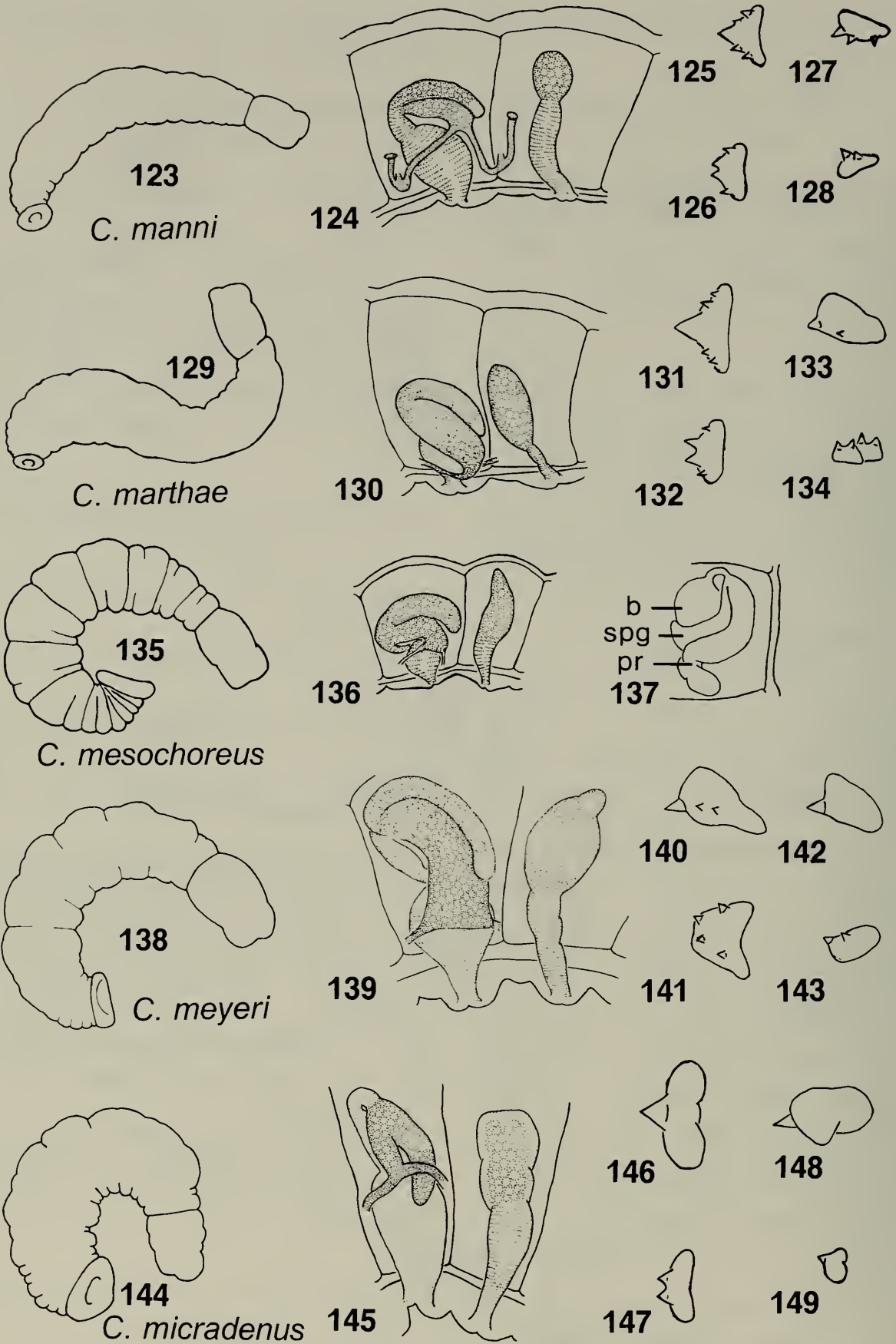
*Types*.—Holotype and 4 paratypes, USNM 29934, additional paratypes, PCH 815, on *Orconectes* sp., from stream 1.5 mi E of Adyville, Perry Co., Indiana, by Perry C. and Virgie F. Holt, 28 Jul 1958.

*Distribution*.—Central Mississippi drainage with disjunct populations in Massachusetts and California (Hoffman 1963:308, Holt 1981a:689).

*Notes*: In Holt, 1981a:689, the last entry in the synonymy should be "*Cambarincola mesochoreus*.—Holt, 1973b:10" instead of "1963:10."

*Cambarincola meyeri* Goodnight, 1942  
Figs. 138–143

*Cambarincola meyeri* Goodnight, 1942:272–273.—Hoffman, 1963:354.—Holt, 1973d:678–682.



Figs. 123-149. 123-128, *Cambarincola manni* Holt; 129-134, *Cambarincola marthae* Holt; 135-137, *Cambarincola mesochoreus* Hoffman, 137, dorsal view of reproductive system, showing recurved prostate; 138-143, *Cambarincola meyeri* Goodnight; 144-149, *Cambarincola micradenus* Holt.

*Types.* — Holotype, USNM 20597, on “*Cambarus bartonii*” [probably *C. b. bartonii* (Fabricius)], from Raven’s Creek, Fayette Co., Kentucky, by Marvin C. Meyer (date unknown).

*Distribution.* — Raven Run (=“Raven’s Creek”), Fayette Co., Kentucky (Holt 1973d: 681).

*Cambarincola micradenus* Holt, 1973  
Figs. 144–149

*Cambarincola micradenus* Holt, 1973b:20–22.

*Types.* — Holotype and 2 paratypes, USNM 45448, 1 paratype, PCH 1615, on *Procambarus paradoxus* (Ortmann), from La Cañada y Tetela de Ocampo, Puebla, México, by Alejandro Villalobos, May 1944.

*Distribution.* — Known only from the type locality.

*Cambarincola montanus* (Goodnight), 1940  
Figs. 150–153

*Triannulata montana* Goodnight 1940:57–58.

*Cambarincola montanus.* — Holt, 1974:67–70; 1981a:690–691.

*Types.* — Holotype, USNM 2056, on *Pacifastacus* sp., from the Kalami River, Washington (Collector and date unknown). Paratypes were left at the University of Illinois in the collections of H. J. Van Cleave (Goodnight 1940:58).

*Distribution.* — Streams of the Coastal and Cascade Ranges of the Pacific drainage in western North America from Santa Barbara Co., California to northern Washington (Holt 1981a:690).

*Cambarincola nanognathus* Holt, 1973  
Figs. 154–159

*Cambarincola nanognathus* Holt, 1973b: 22–23.

*Types.* — Holotype, USNM 45444, 1 paratype, PCH 1830, 1 paratype, IBUM, on

the freshwater crab *Potamocarcinus nicaraguensis*, from Lago de Nicaragua (Isleta de Granada), G. Alvilez, 13 Jul 1964.

*Distribution.* — From southern Veracruz, México, to Nicaragua.

*Cambarincola olmecus* Holt, 1973  
Figs. 160–163

*Cambarincola olmecus* Holt, 1973b:24–26.

*Types.* — Holotype, USNM 45445, 1 paratype, USNM 45446, 1 paratype, PCH 201, 1 paratype, IBUM, on *Procambarus mexicanus* (Erichson), from Tomatlan, Veracruz, México, by Alejandro Villalobos, 3 Nov 1948.

*Distribution.* — San Luis Potosi and Veracruz, México.

*Cambarincola osceolai* Hoffman, 1963  
Figs. 164–165

*Cambarincola osceola* Hoffman, 1963:330–333.

*Cambarincola osceolai.* — Holt, 1973a:93–95; 1973b:10.

*Types.* — Holotype and 7 paratypes, USNM 29943, on *Procambarus paeninsulanus* (Faxon) and *Fallicambarus uhleri* (Faxon) from Dry Creek, 3.1 mi N of Iron City, Seminole Co., Georgia, by Horton H. Hobbs, Jr. and C. W. Hart, Jr., 9 Sep 1955.

*Distribution.* — From southeastern Virginia to northwest peninsular Florida.

Notes: Attention may again be called to the suspicions of both Hoffman (1963:331) and Holt (1973a:94) that *C. osceolai* and *C. vitreus* Ellis, 1918:51 are conspecific.

*Cambarincola ouachita* Hoffman, 1963  
Figs. 166–167

*Cambarincola ouachita* Hoffman, 1963: 303–305.

*Types.* — Holotype, USNM 29937, on *Orconectes* sp., from a small stream 4.3 mi W of the Montgomery Co. line in Chautaugua

Co., Kansas, 8 Jul 1958, by Perry C. and Virgie F. Holt.

*Distribution.*—Known only from the type locality.

Notes: Holt (1973b:9–10) changed the endings of several species to conform to the masculine gender of the generic name *Cambarincola*. He did not emend the name *C. ouachita* which may be considered a noun in apposition, referring to the Ouachita Mountains. Hoffman gives no derivation for the name *ouachita*, but Holt knows he meant it to refer to the mountains.

*Cambarincola pamela* Holt, 1984  
Figs. 168–171

*Cambarincola pamela* Holt, 1984b:544–549.

*Types.*—Holotype, USNM 080687, 4 paratypes, USNM 080688–080691, 10 paratypes, PCH 4065, on *Procambarus clarkii* (Girard), from an irrigation canal that drains into the San Joaquin River in the western part of Stanislaus Co., California, by J. A. Meeuwse, 2 Dec 1982.

*Distribution.*—Stanislaus, Santa Barbara, Merced and Sonoma Counties, California.

Notes: *Cambarincola pamela* has been found only on *P. clarkii*, a crayfish species that has been widely introduced throughout the United States (Hobbs 1989). Therefore, it is possible that *C. pamela* has also been introduced into its present range and that it may be a geographical variant of *C. mesochoreus*, to which it is similar (Holt 1984b).

*Cambarincola philadelphicus* (Leidy, 1851)  
Figs. 172–177

*Astacobdella philadelphia* Leidy, 1851:209.

*Branchiobdella philadelphia*.—Moore, 1893:427–428.

*Bdellodrilus philadelphicus*.—Moore, 1895:497; 1901:542.—Pierantoni, 1912:17.

*Cambarincola philadelphia*.—Ellis, 1912:484.—Hall, 1914:190.—Ellis, 1918:49; 1919:260–263.—Goodnight, 1939:11;

1940:38.—Holt, 1954:169.—Holt & Hoffman, 1959:103.—Hoffman, 1963:341–348.

*Cambarincola philadelphicus*.—Holt, 1973b:9.

*Types.*—Holotype, lost. Topotypes, PCH 695, from Wissahicon Creek in Philadelphia, Pennsylvania (Hoffman 1963:342).

*Distribution.*—From Minnesota and New York south through the Appalachians and Piedmont to South Carolina (Hoffman 1963:344).

Notes: This species is reported in the literature as unusually variable. Indeed, in southwestern Virginia it appears to be so, but many references to it undoubtedly apply to other related forms. The problem of variability in *C. philadelphicus* should be re-studied.

*Cambarincola restans* Hoffman, 1963  
Figs. 178–179

*Cambarincola restans* Hoffman, 1963:305–307.

*Types.*—Holotype and 2 paratypes, USNM 29938, on *Orconectes* sp., from Sugar Creek, 2 mi N of Avoca, Benton Co., Arkansas, by Perry C. and Virgie F. Holt, 6 Jul 1958.

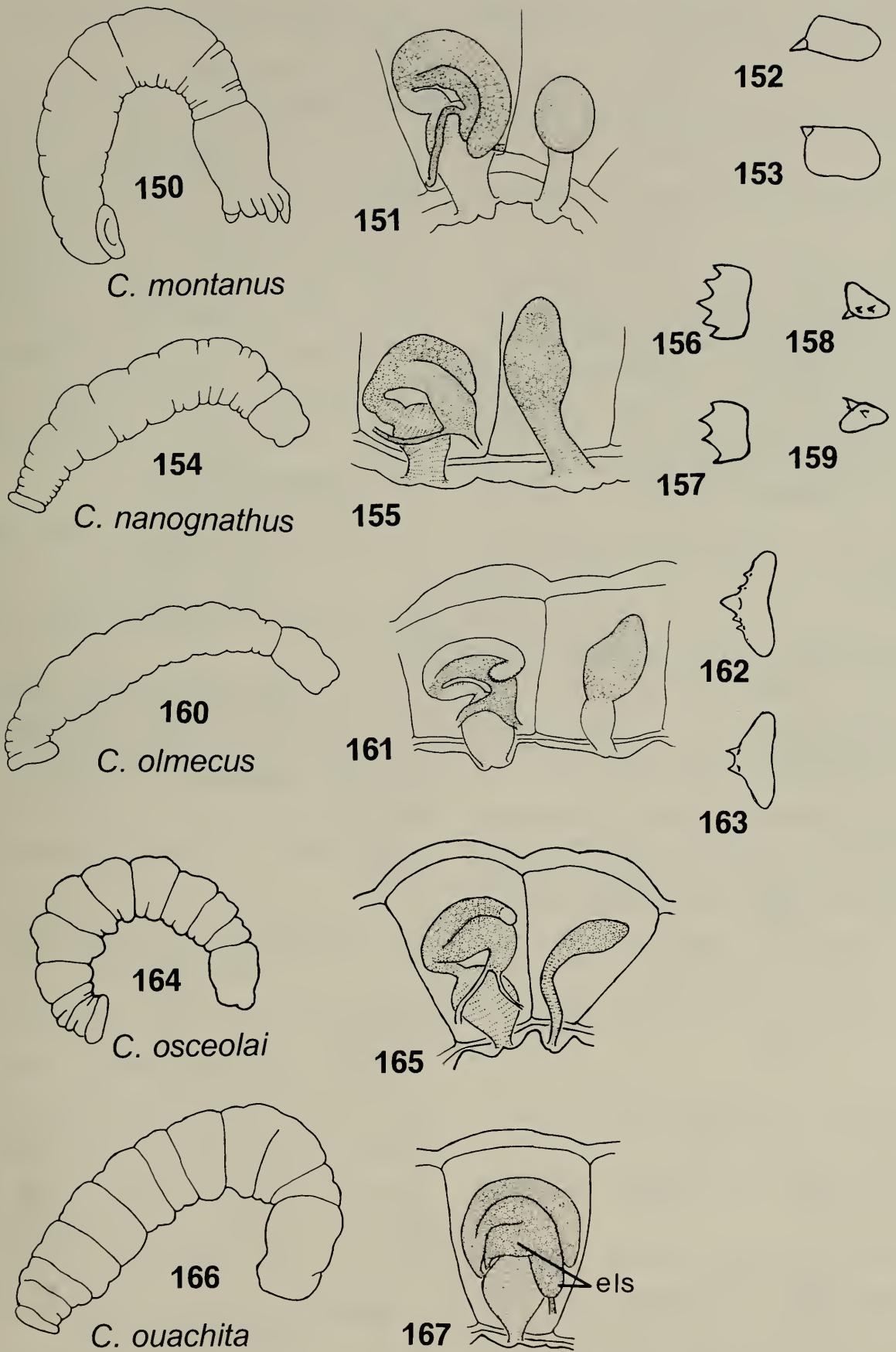
*Distribution.*—Known only from the type locality.

*Cambarincola serratus* Holt, 1981  
Figs. 180–183

*Cambarincola serratus* Holt, 1981a:691–693.

*Types.*—Holotype, USNM 54638; 3 paratypes, PCH 795, on *Pacifastacus connectens* (Faxon), from Idaho State Fish Hatchery, Riley Creek, Gooding Co., Idaho, by Perry C. and Virgie F. Holt, 14 Jul 1958; 2 paratypes, PCH 784, on *P. connectens*, from spring tributary to Snake River, Hagerman, Gooding Co., Idaho, by Perry C. and Virgie F. Holt, 14 Jul 1958.





Figs. 150–167. 150–153, *Cambarincola montanus* Goodnight; 154–159, *Cambarincola nanognathus* Holt; 160–163, *Cambarincola olmecus* Holt; 164–165, *Cambarincola osceolai* Hoffman; 166–167, *Cambarincola ouachita* Hoffman.

*Distribution.*—Tributaries of the Snake River, Gooding Co., Idaho.

*Cambarincola sheltensis* Holt, 1973  
Figs. 184–189

*Cambarincola sheltensis* Holt, 1973c:229–231.

*Types.*—Holotype, USNM 49683, 2 paratypes, PCH 1846, on *Orconectes australis australis* (Rhoades), from Shelta Cave, Huntsville, Madison Co., Alabama, by John E. and Martha Cooper, 24 Aug 1963; 2 paratypes, USNM 49684, 1 paratype, PCH 1863, on *O. a. australis*, from Shelta Cave, Madison Co., Alabama, by James E. Larimer, 1965.

*Distribution.*—Known only from the type locality.

*Cambarincola shoshone* Hoffman, 1963  
Figs. 190–191

*Cambarincola shoshone* Hoffman, 1963: 319–320.—Holt, 1981a:693.

*Types.*—Holotype and 3 paratypes, USNM 29941, topotypes, PCH 785, on *Pacifastacus connectens* (Faxon), from Riley Creek (Idaho State Fish Hatchery), Hagerman, Gooding Co., Idaho, by Perry C. and Virgie F. Holt, 14 Jul 1958.

*Distribution.*—Known only from the type locality.

*Cambarincola smalleyi* Holt, 1964  
Figs. 192–195

*Cambarincola smalleyi* Holt, 1964:1–4; 1973b:26–27.

*Types.*—Holotype, USNM 20940, 1 paratype, 30941, 1 paratype in the collections of Tulane University, 1 paratype, PCH 1702, on the freshwater crab *Pseudothelphusa tuminenus*, from Río Hondura, 8 mi N of San Jeronimo de Moravia, San José Province, Costa Rica, by A. E. Smalley, 9 Jul 1962.

*Distribution.*—Known only from the type locality.

Notes: Holt (1964:3) postulated that *C. smalleyi* was carried to Costa Rica by cambarines and qualified (Holt 1973b:27) this conclusion by suggesting that the transfer to crabs could have occurred much further north in México. In truth we know too little to make any credible conjectures about the ancient origin and subsequent wanderings of branchiobdellidans. They may as easily have originated as symbionts of freshwater crabs and shrimps and later taken up a symbiotic relationship with crayfishes. *Cambarincola smalleyi* is the southernmost known species of the family.

*Cambarincola speocirolanae* Holt, 1984  
Figs. 196–199

*Cambarincola speocirolanae* Holt, 1984a: 36–38.

*Types.*—Holotype, USNM 80221, 1 paratype, PCH 4054, on the isopod *Speocirolana palaezi*, from Sotao del Arroyo, San Luis Potosí, México, by Peter Sprouse, 22 Feb 1980.

*Distribution.*—Known only from the type locality.

*Cambarincola steevesi* Holt, 1973  
Figs. 200–203

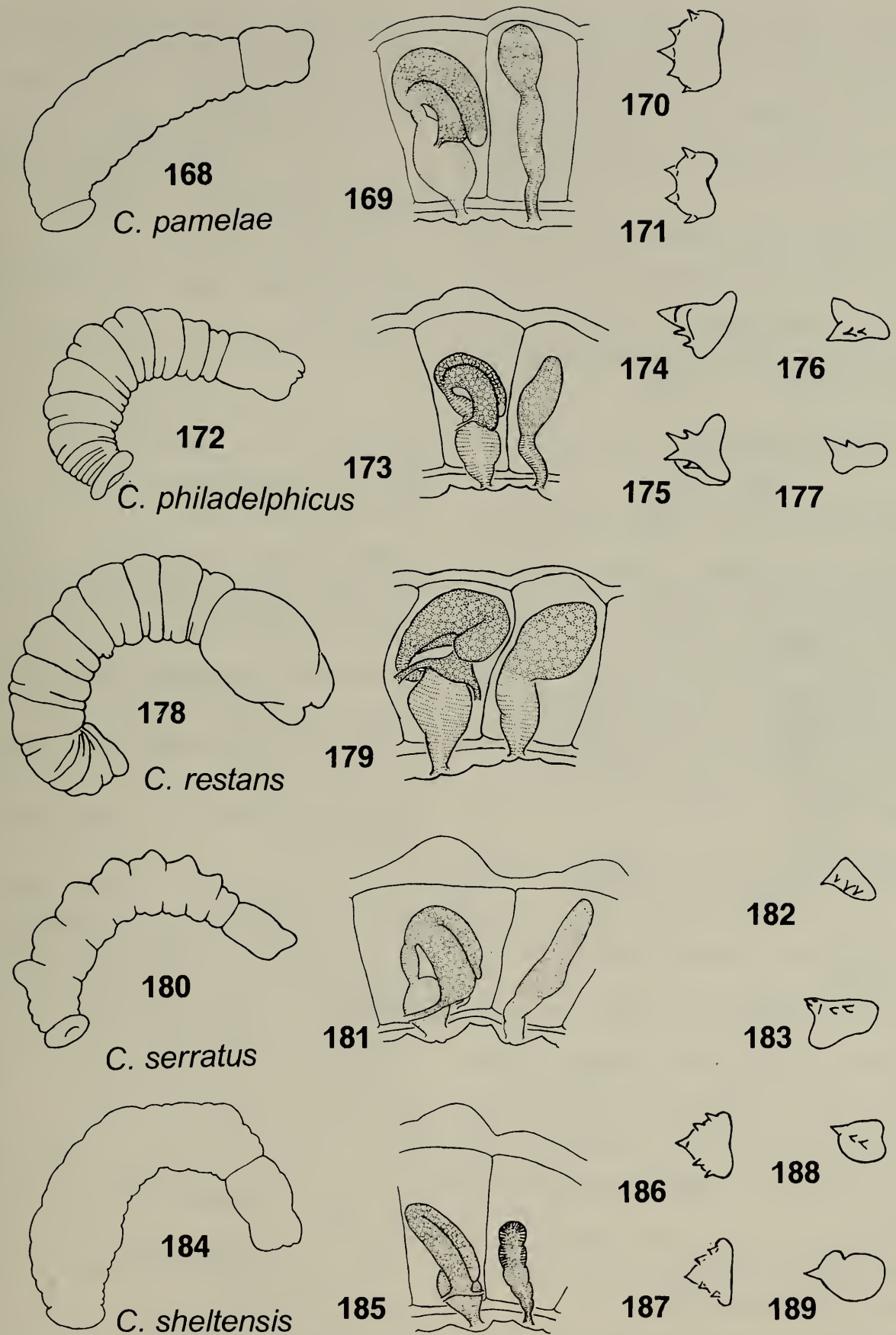
*Cambarincola steevesi* Holt, 1973c:224–226.

*Types.*—Holotype, USNM 40680, 2 paratypes, USNM 40681, 1 paratype, PCH 1883, on the isopod *Asellus alabamensis* (Stafford), from Glover's Cave, Todd Co., Kentucky, by R. M. Norton, 17 Apr 1964; 1 paratype, USNM 49682, on *Asellus alabamensis*, from Brown Cave, Barren Co., Kentucky, by R. M. Norton, 25 Sep 1965.

*Distribution.*—The type locality and Taylor Cave, Trigg Co., Kentucky.

*Cambarincola susanae* Holt, 1973  
Figs. 204–207

*Cambarincola susanae* Holt, 1973b:27–29.



Figs. 168–189. 168–171, *Cambarincola pamelae* Holt; 172–177, *Cambarincola philadelphicus* (Leidy); 178–179, *Cambarincola restans* Hoffman; 180–183, *Cambarincola serratus* Holt; 184–189, *Cambarincola sheltensis* Holt.

*Types.*—Holotype and 2 paratypes, USNM 45441, 10 paratypes, PCH 1529, 3 paratypes, IBUM, on *Procambarus acutus cuevachicae* (Hobbs), from Cueva Chica, El Pujal, 3 km NE of Valles, San Luis Potosí, México, by Alejandro Villalobos, 9 May 1950.

*Distribution.*—In eastern México from Rio San Juan, Nuevo Leon to western Campeche.

Notes: *Cambarincola susanae* may be an ectoparasite in the gill chambers of the host (Holt 1973b:29).

*Cambarincola toltecus* Holt, 1973  
Figs. 208–211

*Cambarincola toltecus* Holt, 1973b:29–31.

*Types.*—Holotype, USNM 45436, 2 paratypes, USNM 45437, 2 paratypes, IBUM, 2 paratypes, PCH 697, on the freshwater crab *Pseudothelphusa veracruzana*, from Rio Tapalapa, Santiago, Tuxtla, Veracruz, México, by Alejandro Villalobos and Horton H. Hobbs, Jr., 17 Apr 1957.

*Distribution.*—Tropical lowlands of Veracruz, México.

*Cambarincola virginicus* Hoffman, 1963  
Figs. 212–215

*Cambarincola virginica* Hoffman, 1963: 322–323.

*Cambarincola virginicus.*—Holt, 1973b:10.

*Types.*—Holotype and 1 paratype, USNM 29942, on *Cambarus acuminatus* Faxon, from a small, slow stream 4.7 mi N of Petersburg, Chesterfield Co., Virginia, by Marvin L. Bobb and Perry C. Holt, 31 May 1949.

*Distribution.*—Along the Fall Line in eastern Virginia (Hoffman 1963:323) and eastern North Carolina.

*Cambarincola vitreus* Ellis, 1918  
Figs. 216–217

*Cambarincola vitrea* Ellis, 1918:49–51; 1919:257–258.—Goodnight, 1940:33–34;

1943:100.—Holt & Hoffman, 1959: 103.—Hoffman, 1963:324–329.

*Cambarincola vitreus.*—Holt, 1973b:9.

*Types.*—Holotype, USNM 17667, on *Orconectes immunis* (Hagen), from Douglas Lake, Cheboygan Co., Michigan, by Max M. Ellis, Jul 1915.

*Distribution.*—Western portions of the upper Mississippi valley from north and west of Arkansas.

Notes: See *Cambarincola osceola*.

*Ceratodrilus* Hall, 1914

*Ceratodrilus* Hall, 1914:190–191.

*Ceratodrilus* Stephenson, 1930:901.

*Cirrodrilus* Goodnight, 1940:63–64 [in part].

*Type species.*—*Ceratodrilus thysanosomus* Hall, 1914, by original designation.

*Gender.*—Masculine.

*Ceratodrilus ophiorhysis* Holt, 1960  
Figs. 218–221

*Ceratodrilus ophiorhysis* Holt, 1960a:60 (incorrect spelling).

*Ceratodrilus ophiorhysis.*—Holt, 1960a:61; 1988a:308.

*Types.*—Holotype, USNM 29910, 4 paratypes, USNM 29911, 3 paratypes, PCH 786, on *Pacifastacus gambelii* (Girard), from the Snake River between Buhl and Wendel, Gooding Co., Idaho, by Perry C. and Virgie F. Holt and Judson Ford, 14 Jul 1958.

*Distribution.*—The Snake River and its tributaries in Idaho and Oregon.

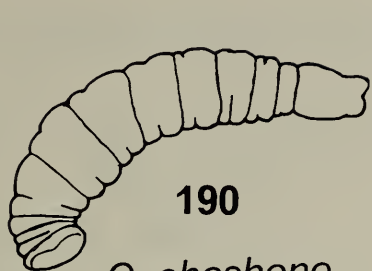
*Ceratodrilus thysanosomus* Hall, 1914  
Figs. 222–223

*Ceratodrilus thysanosomus* Hall, 1914: 191.—Stephenson, 1930:801.—Yamaguchi, 1932:367.

*Cirrodrilus thysanosomus.*—Goodnight, 1940:64–65 [in part].

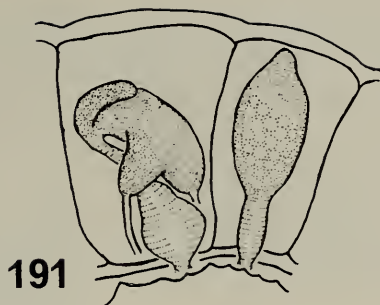
*Ceratodrilus thysanosomus.*—Holt, 1960a: 58–60.

*Types.*—Holotype, USNM 17708, from

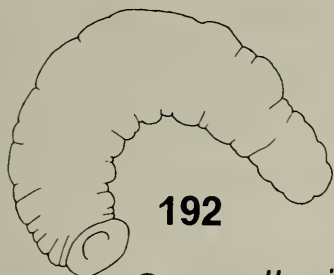


190

*C. shoshone*



191



192

*C. smalleyi*



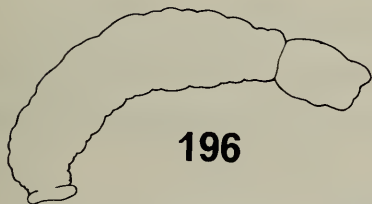
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194



195



196

*C. speocirolanae*



197



198

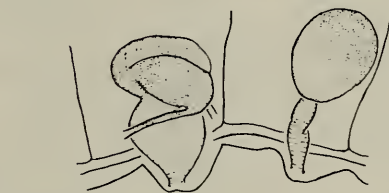


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200

*C. steevesi*



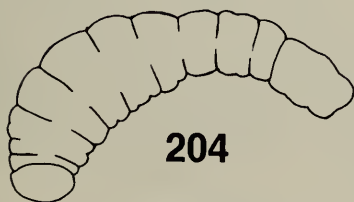
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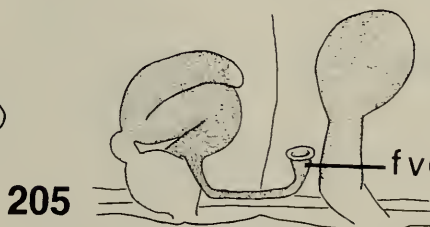


203



204

*C. susanae*



205

fve 206



207



Figs. 190–207. 190–191, *Cambarincola shoshone* Hoffman; 192–195, *Cambarincola smalleyi* Holt; 196–199, *Cambarincola speocirolanae* Holt; 200–203, *Cambarincola steevesi* Holt; 204–207, *Cambarincola susanae* Holt.

streams of Great Basin, Salt Lake City, Utah (no date).

*Distribution.*—Streams of the Great Salt Lake Basin.

Notes: The two species of *Ceratodrilus* differ only in the length of their dorsal appendages (Holt 1960a); their distinctiveness should be reinvestigated.

*Ellisodrilus* Holt, 1960

*Ellisodrilus* Holt, 1960b:170.

*Type species.*—*Ellisodrilus clitellatus* Holt, 1960, by original designation.

*Gender.*—Masculine.

*Ellisodrilus carronamus* Holt, 1988  
Figs. 224–227

*Ellisodrilus carronamus*, 1988b:796–798.

*Types.*—Holotype, USNM 119539, 2 paratypes, USNM 119540–119541, on *Orconectes* sp., from Carr Creek, Overton Co., Tennessee, ca. 3 mi S of Livingston, on State Highway 42, by Perry C. and Virgie F. Holt, 26 Jul 1961.

*Distribution.*—Carr Creek and Roaring River, Overton Co., Tennessee.

Notes: There appears to be a N–S gradient in *Ellisodrilus* species with *E. carronamus* the southern-most, *E. durbini* the northern-most and *E. clitellatus* found in between. This occurs in part in areas scoured by the Pleistocene glaciation (Holt 1960b:171, 174; 1988b:798).

*Ellisodrilus clitellatus* Holt, 1960  
Figs. 228–231

*Ellisodrilus clitellatus* Holt, 1960b:169–176.

*Types.*—Holotype, USNM 29935, 1 paratype, USNM 29936, 18 paratypes, PCH 827, on *Cambarus distans* Rhoades, from stream 8.9 mi E of Columbia on Kentucky Highway 80, Adair Co., Kentucky, by Perry C. and Virgie F. Holt, 28 Jul 1958.

*Distribution.*—Kentucky.

Notes: The first paragraph on page 171

(Holt 1960b) should be transposed to follow the diagnosis of the genus on page 170.

*Ellisodrilus durbini* (Ellis, 1918)  
Figs. 232–234

*Pterodrilus durbini* Ellis, 1918:49.—Ellis 1919:254.—Goodnight 1940:61–62.  
*Ellisodrilus durbini.*—Holt, 1960b:173.

*Types.*—Holotype, USNM 17655, on *Orconectes barrenensis* Rhoades, from White River, at Irondale, Anderson Co., Indiana.

*Distribution.*—From Anderson Co., Indiana, into Michigan (Ellis 1918:50).

*Magmatodrilus* Holt, 1967

*Stephanodrilus* Goodnight, 1940:55 [in part].

*Magmatodrilus* Holt, 1967b:3–4.

*Type species.*—*Magmatodrilus obscurus* (Goodnight, 1940), by original designation.

*Gender.*—Masculine.

*Magmatodrilus obscurus* (Goodnight, 1940)  
Figs. 235–238

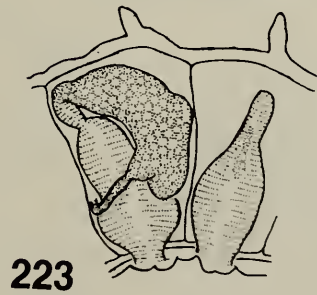
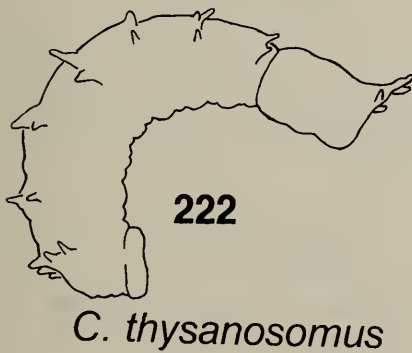
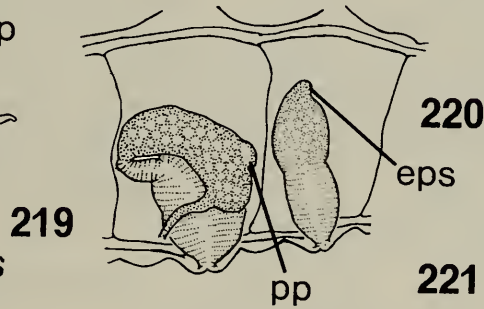
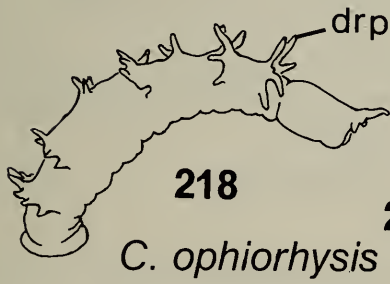
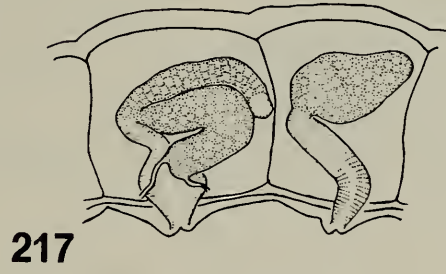
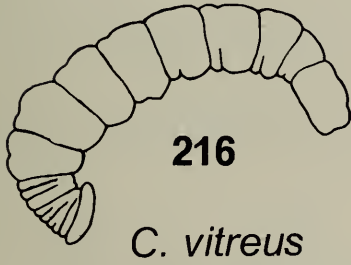
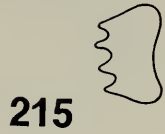
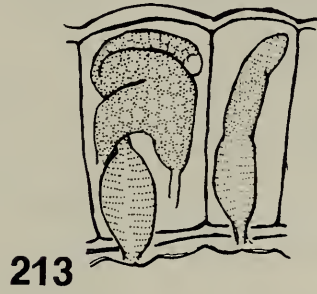
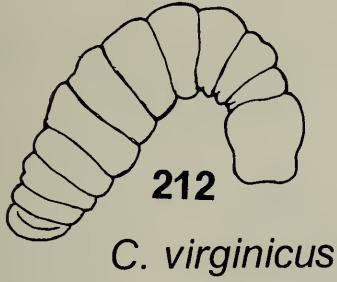
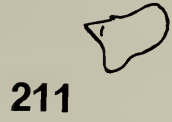
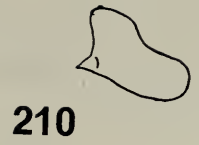
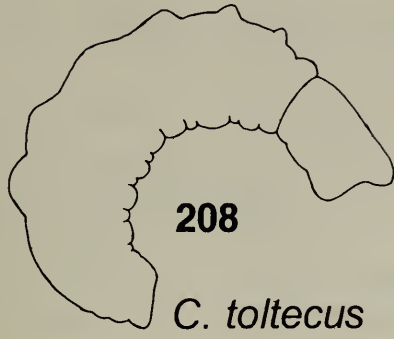
*Stephanodrilus obscurus* Goodnight, 1940:55–56.

*Magmatodrus obscurus.*—Holt, 1967b:4–5.

*Types.*—Holotype, USNM 20568, on *Pacifastacus nigrescens* (Stimpson) (Goodnight, 1940:55), (collector and date unknown), from Fall River, Shasta Co., California; 2 topotypes, USNM 45696, 11 topotypes, PCH 1818, on unknown host, from the head of Fall River, Thousand Springs Ranch, Shasta Co., California, by Perry C. and Virgie F. Holt, Aug 1964.

*Distribution.*—Known only from the type locality.

Notes: Some ambiguity may exist as to the type locality. Holt was refused permission to trap for crayfish in Fall River by the local game warden. The river is a deep, ditch-like stream that does not lend itself to collecting with a dipnet. After several futile attempts to do so, the Holts obtained per-



Figs. 208-223. 208-211, *Cambarincola toltecus* Holt; 212-215, *Cambarincola virginicus* Hoffman; 216-217, *Cambarincola vitreus* Ellis; 218-221, *Ceratodrilus ophiorhysis* Holt; 222-223, *Ceratodrilus thysanosomus* Hall.

mission to take a collection from the spring from which Fall River arises. The holotype and topotypes appear to be identical (Holt 1967b:4–5).

*Oedipodrilus* Holt, 1967

*Oedipodrilus* Holt, 1967a:58.

*Type species.*—*Oedipodrilus oedipus* Holt, 1967a, by original designation.

*Gender.*—Masculine.

*Oedipodrilus anisognathus* Holt, 1988  
Figs. 239–242

*Oedipodrilus anisognathus* Holt, 1988b:  
798–800.

*Types.*—Holotype, USNM 119534, 1 paratype, USNM 119535, on *Orconectes* sp., from a small stream in Montgomery Bell State Park, Dickson Co., Tennessee, by Perry C. and Virgie F. Holt, 4 Jul 1958; 3 paratypes, USNM 119536–119537, on *Orconectes* sp., from Carr Creek, ca. 3.0 mi S of Livingston, Overton Co., Tennessee, by Perry C. and Virgie F. Holt, 26 Jul 1961.

*Distribution.*—Dickson and Overton Counties, Tennessee, the Central (Nashville) Basin and the eastern Highland Rim, respectively (Holt 1988b:800).

*Oedipodrilus cuetzalanae* Holt, 1984  
Figs. 243–246

*Oedipodrilus cuetzalanae* Holt, 1984a:38–41.

*Types.*—Holotype, USNM 80223, 8 paratypes, PCH 4050, on *Procambarus cuetzalanae* Hobbs, from Sima Zoquiapan, 1.1 km N of Cuetzalan, Puebla, México, by L. Wilk, W. Hooper and M. Minton, 2 Jan 1980.

*Distribution.*—Known only from the type locality.

*Oedipodrilus macbaini* (Holt, 1955)  
Figs. 247–248

*Cambarincola macbaini* Holt, 1955:27–31.

*Oedipodrilus macbaini.*—Holt, 1969:205; 1984a:39; 1988b:800–804.

*Types.*—Holotype, USNM 25952, 6 paratypes, PCH 134, on *Orconectes* sp., from Charles Creek, 8 mi W of Ashland, on State Highway 5, Boyd Co., Kentucky, by Rodney Macbain, Jul 1948.

*Distribution.*—Known only from the type locality.

*Oedipodrilus oedipus* Holt, 1967  
Figs. 249–252

*Oedipodrilus oedipus* Holt, 1967a:58–60.

*Types.*—Holotype, USNM 34086, 7 paratypes, USNM 34087, 4 paratypes, PCH 756, on *Orconectes compressus* (Faxon), collected 10.2 mi E of Waverly, Humphreys Co., by Perry C. and Virgie F. Holt, 5 Jul 1958.

*Distribution.*—Known only from the type locality.

*Pterodrilus* Moore, 1894

*Pterodrilus* Moore, 1894:449–450.

*Type species.*—*Pterodrilus alcicornus* Moore, 1894, subsequent designation by Goodnight (1940).

*Gender.*—Masculine.

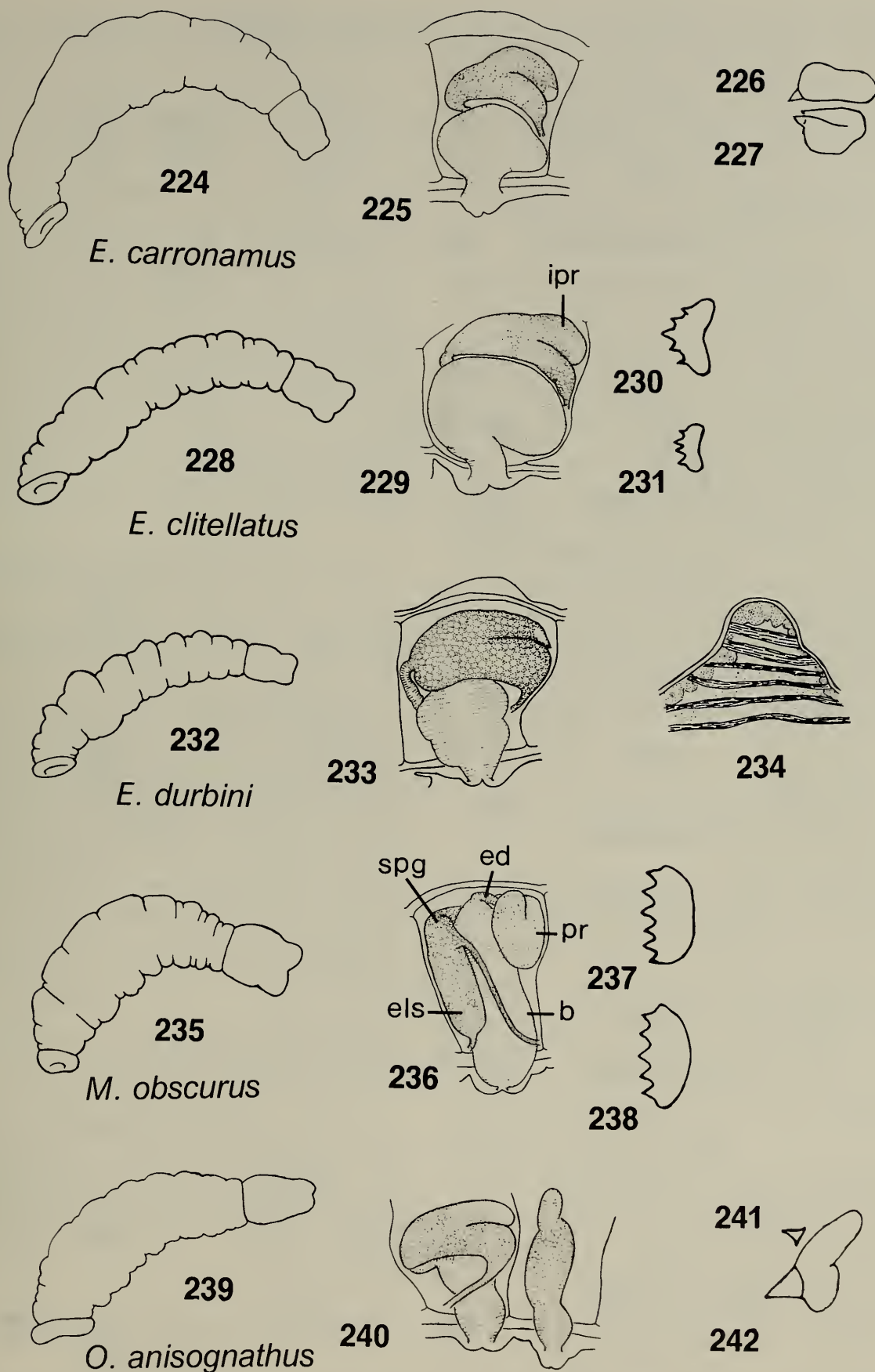
*Pterodrilus alcicornus* Moore 1894  
Figs. 253–254

*Pterodrilus alcicornus* Moore, 1894:450–453.—Pierantoni, 1912:25.—Ellis, 1919:245.—Goodnight, 1940:58–60.—Holt, 1968c:6–12.

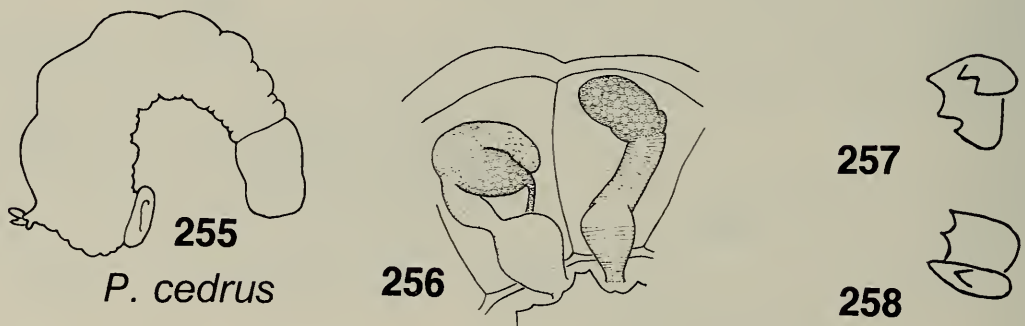
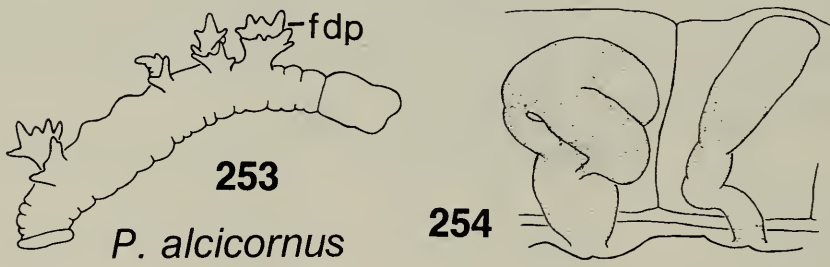
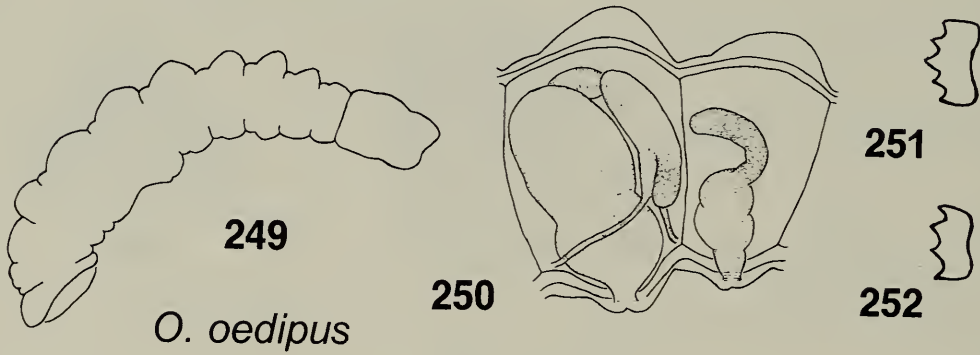
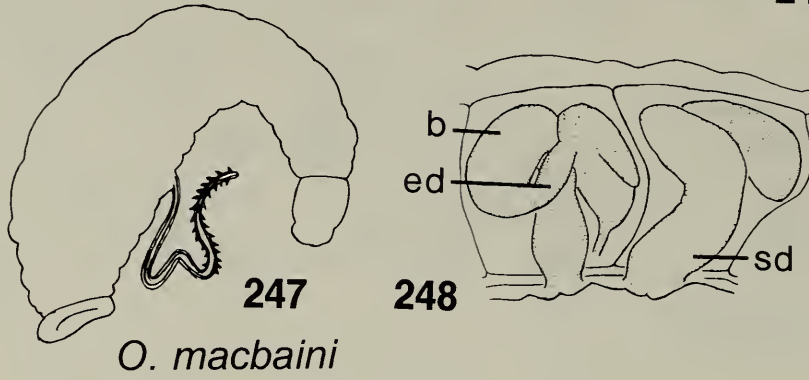
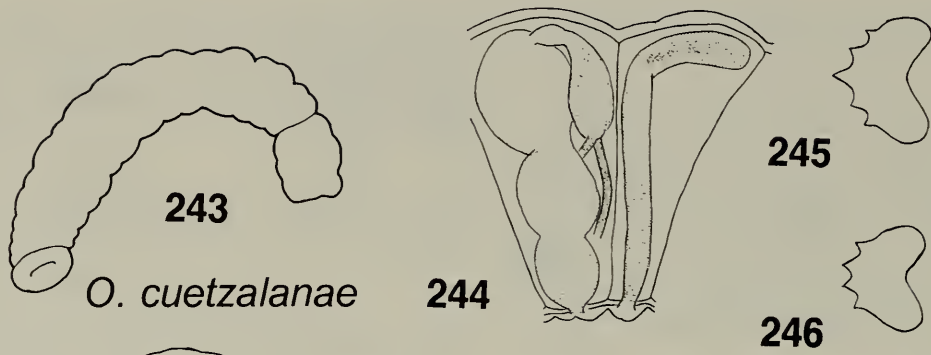
*Types.*—Apparently lost (Holt 1968c:6), but was on *Cambarus acuminatus* Faxon, from Johns River at Blowing Rock, Watauga Co., North Carolina, in the summer of 1893, presumably by Moore himself (Moore 1894:453).

*Distribution.*—The mountain streams of the Southern Appalachians in Virginia, North Carolina, Tennessee, and West Vir-





Figs. 224-242. 224-227, *Ellisodrilus carronamus* Holt; 228-231, *Ellisodrilus clitellatus* Holt; 232-234, *Ellisodrilus durbini* (Ellis), 234, longitudinal section through a dorsal ridge, showing supernumerary muscles; 235-238, *Magmatodrilus obscurus* (Goodnight); 239-242, *Oedipodrilus anisognathus* Holt.



Figs. 243-258. 243-246, *Oedipodrilus cuetzalanae* Holt; 247-248, *Oedipodrilus macbaini* (Holt); 249-252, *Oedipodrilus oedipus* Holt; 253-254, *Pterodrilus alcicornus* Moore; 255-258, *Pterodrilus cedrus* Holt.

ginia (Holt 1968c:12) in which the species is abundant.

*Pterodrilus cedrus* Holt, 1968  
Figs. 255–258

*Pterodrilus cedrus* Holt, 1968c:21–23.

*Types.*—Holotype and 5 paratypes, USNM 36464, 3 paratypes, PCH 1396, on *Orconectes placidus* (Hagen) and *Cambarus tenebrosus* Hay, from a small stream at the intersection of State Highways 51 and 53 in Celina, Clay Co., Tennessee, by Perry C. and Virgie F. Holt, 25 Jul 1961.

*Distribution.*—The eastern Highland Rim and Nashville Basin regions of Tennessee.

*Pterodrilus choritonamus* Holt, 1968  
Figs. 259–262

*Pterodrilus choritonamus* Holt, 1968c:26–28.

*Types.*—Holotype, USNM 36471, 2 paratypes, USNM 36472, on *Cambarus tenebrosus* Hay, from a tributary (Holt Spring Branch) ca. 4.5 mi N of Livingston, Overton Co., Tennessee, by Perry C. and Virgie F. Holt, 24 Jul 1961; 5 paratypes, PCH 1393, on *C. tenebrosus* and *Orconectes placidus* (Hagen), from Little Eagle Creek, Overton Co., Tennessee, by Perry C. and Virgie F. Holt, 24 Jul 1961.

*Distribution.*—Tributaries of the Cumberland River in the eastern Highland Rim region in Tennessee (see locality records for *Pterodrilus* manuscript by Holt in the Library of Congress and the USNM). Some conspecific material is deposited in the National Museum of Natural History, USNM 36473–36476.

*Pterodrilus distichus* Moore, 1894  
Figs. 263–266

*Pterodrilus distichus* Moore 1894:453–454.—Pierantoni, 1912:25.—Hall, 1914:190.—Ellis, 1919:254.—Goodnight, 1940:60; 1943:100.—Holt, 1968c:12.

*Types.*—From western New York, location unknown (Holt 1968c:12).

*Distribution.*—Ohio, Mississippi, Great Lakes, drainage systems in Kentucky, Ohio, Indiana, Illinois, Michigan, and New York.

*Pterodrilus hobbsi* Holt, 1968  
Figs. 267–270

*Pterodrilus hobbsi* Holt, 1968c:18.

*Types.*—Holotype, USNM 36486, 5 paratypes, USNM 36487, on *Cambarus rusticiformis* Rhoades, *Orconectes rusticus* (Girard), and *Orconectes placidus* (Hagen), from Spring Creek, 1.4 mi N of the Putnam Co. line on State Highway 42, Overton Co., Tennessee, by Perry C. and Virgie F. Holt, 26 Jul 1961.

*Distribution.*—Cumberland River in Tennessee and Kentucky, the upper Tennessee drainage in Tennessee, the New River drainage in Virginia and North Carolina, the Big Sandy drainage in Virginia (Holt 1968c:20, 38)

*Pterodrilus mexicanus* Ellis, 1919  
Figs. 271–272

*Pterodrilus mexicanus* Ellis, 1919:254.—Goodnight, 1940:63.—Holt, 1968c:15; 1973b:32.

*Types.*—Holotype, USNM 17654, on *Procambarus mexicanus* (Erichson), from Mirador, Veracruz, México, by Nelson and Goldman.

*Distribution.*—Mountains of Arkansas, Oklahoma, and Missouri.

Notes: The apparent disjunct distribution of this species is difficult to explain. Hobbs (1989) lists the type locality of *P. mexicanus* as “El Mirador de Zacuapan, 8 km NE of Huatusco, Veracruz, México.” However, Holt was unable to find *P. mexicanus* in Mexico (Holt 1973b:32).

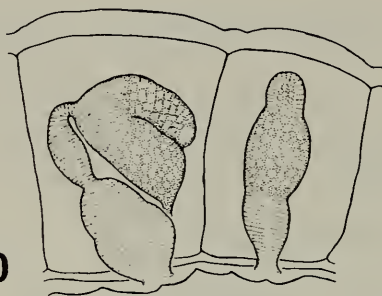
*Pterodrilus missouriensis* Holt, 1968  
Figs. 273–274

*Pterodrilus missouriensis* Holt, 1968c:28–32.



259

*P. choritonamus*



260

261

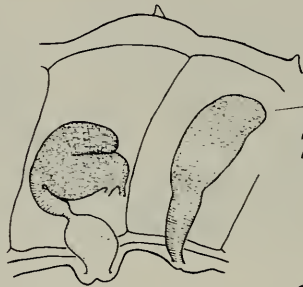


262



263

*P. distichus*

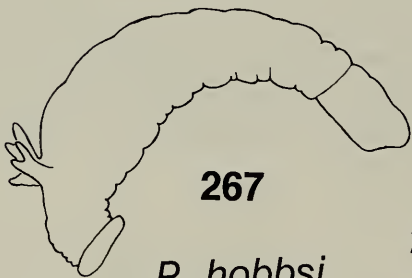


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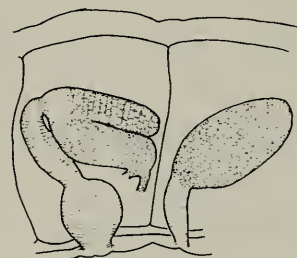


266



267

*P. hobbsi*

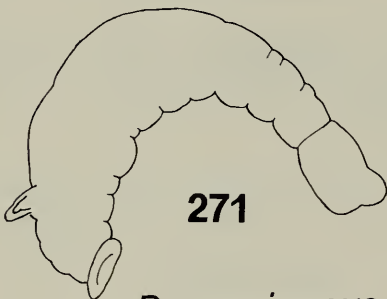


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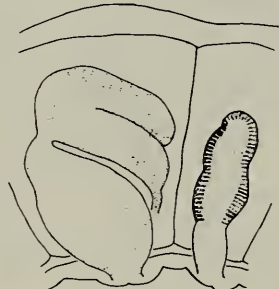


270



271

*P. mexicanus*

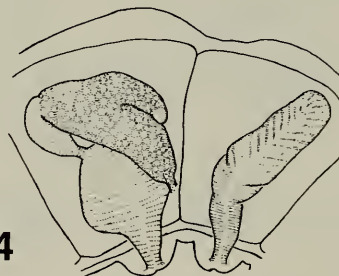


272



273

*P. missouriensis*



274

Figs. 259-274. 259-262, *Pterodrilus choritonamus* Holt; 263-266, *Pterodrilus distichus* Moore; 267-270, *Pterodrilus hobbsi* Holt; 271-272, *Pterodrilus mexicanus* Ellis; 273-274, *Pterodrilus missouriensis* Holt.

*Types.* — Holotype, USNM 36469, 2 paratypes, USNM 36470, 2 paratypes, PCH 1476, on *Orconectes luteus* (Creaser), from Whetstone Creek, 5 mi W of Mountain Grove, Wright Co., Missouri, by Perry C. Holt, 23 Aug 1961.

*Distribution.* — Known only from the type locality.

*Pterodrilus simondsi* Holt, 1968  
Figs. 275–276

*Pterodrilus simondsi* Holt, 1968c:23–26.

*Types.* — Holotype, USNM 26477, 5 paratypes, USNM 36478, 4 paratypes, PCH 989, on *Cambarus bartonii bartonii* (Fabricius), from a tributary to the Oconee River S of Morganton, Fannin Co., Georgia, by Kenneth W. Simonds, 6 Nov 1958.

*Distribution.* — Tributaries to the Oconee River in Fannin and Union Counties, Georgia and Cherokee Co., North Carolina.

*Sathodrilus* Holt, 1968

*Sathodrilus* Holt, 1968b:294.

*Type species.* — *Sathodrilus carolinensis* Holt, 1968, by original designation.

*Gender.* — Masculine.

*Sathodrilus attenuatus* Holt, 1981  
Figs. 277–280

*Sathodrilus attenuatus* Holt, 1981b:849–853.

*Types.* — Holotype, USNM 65227, 26 paratypes, PCH 1113, on *Pacifastacus leniusculus klamathensis* (Stimpson), from Elk Creek, ca. 12.6 mi S of Cottage Grove, Douglas Co., Oregon, by Perry C. and Virgie F. Holt, 11 Jul 1960.

*Distribution.* — Streams of the Cascade and Coastal Ranges in Oregon and Washington to the headwater streams of the Snake River in Wyoming.

*Sathodrilus carolinensis* Holt, 1968  
Figs. 281–284

*Sathodrilus carolinensis* Holt, 1968b:296–299.

*Types.* — Holotype, USNM 37107, 1 paratype, USNM 37108, 1 paratype, PCH 1333, on *Cambarus latimanus* (Le Conte) and *Cambarus* sp., from a small stream ca. 11.5 mi SW of Anderson, Anderson Co., South Carolina, on U.S. Highway 29, by Perry C. and Virgie F. Holt, 21 Mar 1961.

*Distribution.* — Known only from the type locality.

*Sathodrilus chehalisae* Holt, 1981  
Figs. 285–286

*Sathodrilus chehalisae* Holt, 1981b:853–855.

*Types.* — Holotype and 7 paratypes, USNM 65228, 3 paratypes, PCH 1813, on *Pacifastacus leniusculus trowbridgii* (Stimpson), from Chehalis River at Adna, Lewis Co., Washington, by Perry C. and Virgie F. Holt, 15 Aug 1964.

*Distribution.* — Known only from the type locality.

*Sathodrilus dorfus* Holt, 1977  
Figs. 287–290

*Sathodrilus dorfus* Holt, 1977:120–122.

*Types.* — Holotype, USNM 53643, 3 paratypes, PCH 1120, on *Pacifastacus leniusculus klamathensis* (Stimpson), from a small tributary to the Yaguina River, 13.4 km NE of Toledo, Lincoln Co., Oregon, by Perry C. and Virgie F. Holt, 12 Jul 1960.

*Distribution.* — Known only from the type locality.

*Sathodrilus elevatus* (Goodnight, 1940)  
Figs. 291–294

*Cambarincola elevata* Goodnight, 1940:34–35.

*Cambarincola ? elevata.* — Hoffman, 1963:275.

*Sathodrilus elevatus.* — Holt, 1978:473–481.

*Types.*—Holotype, on *Orconectes virilis* Hagen, from Leaf River, Illinois; paratypes, on *O. virilis*, from: Macoupin Creek near Carlinville, Illinois; Buck Creek, near Penfield, Illinois; Leaf River, near Bryon, Illinois; Seven Mile Creek, Rock River drainage, Illinois; and Lake Geneva, Wisconsin.

*Distribution.*—The upper Mississippi and Red Rivers and Great Lakes drainages in Illinois, Indiana, Iowa, Michigan, Minnesota, South Dakota, Wisconsin in the United States and Ontario, Canada (Holt 1978: 478–481).

*Notes:* The redescription of *Sathodrilus elevatus* and the determination that it is conspecific with Goodnight's holotype were based upon the comparison of the holotype and numerous specimens from the localities listed by Holt (1978:479–481). Goodnight's material, including types, was lost (Goodnight, pers. comm.).

*Sathodrilus hortonii* Holt  
Figs. 295–298

*Sathodrilus hortonii* Holt, 1973a:97–99.

*Types.*—Holotype, USNM 48713, 2 paratypes, USNM 49714, 2 paratypes, PCH 2716, on *Cambarus diogenes* Girard and *Cambarus* sp., from Pond Creek, 2.1 mi NE of Laurel Hill, Okaloosa Co., Florida, by Horton H. Hobbs, III, 10 Aug 1968.

*Distribution.*—Known only from the type locality.

*Sathodrilus inversus* (Ellis, 1919)  
Figs. 299–302

*Cambarincola inversa* Ellis, 1919:259–260.

*Cambarincola ? inversa.*—Hoffman, 1963: 294.

*Sathodrilus virgiliae.*—Holt, 1977:128–131.

*Sathodrilus inversus.*—Holt, 1981b:855–856.

*Types.*—Holotype, USNM 16780, 5 paratypes, USNM 17680, Eugene, Oregon, on *Pacifastacus leniusculus klamathensis*

(Stimpson), from Eugene, Oregon, by J. E. Gutberlet.

*Distribution.*—Common in streams of the Pacific versant in Oregon and Washington.

*Sathodrilus lobatus* Holt, 1977  
Figs. 303–306

*Sathodrilus lobatus* Holt, 1977:122–125.

*Types.*—Holotype and 3 paratypes, USNM 53644, 5 paratypes, PCH 1117, on *Pacifastacus leniusculus klamathensis* (Stimpson), from Mary's River, 7.7 km E of Blodgett, Benton Co., Oregon, by Perry C. and Virgie F. Holt, 12 Jul 1960.

*Distribution.*—Western Oregon and Washington (Holt 1977:125).

*Sathodrilus megadenus* Holt, 1968  
Figs. 307–310

*Sathodrilus megadenus* Holt, 1968b:302–305.

*Types.*—Holotype, USNM 37109, 2 paratypes, USNM 37110, 2 paratypes, PCH 1346, on *Cambarus latimanus* (Le Conte), from a small stream, 3.1 mi N of Buchanan, Haralson Co., Georgia, by Perry C. and Virgie F. Holt, 25 Mar 1961.

*Distribution.*—Known only from the type locality.

*Sathodrilus nigrofluvius* Holt, 1989  
Figs. 311–314

*Sathodrilus nigrofluvius* Holt, 1989b:738–741.

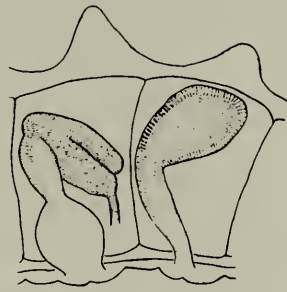
*Types.*—Holotype, USNM 118199, 3 paratypes, USNM 118200–118202, on unknown host, from a tributary of the Black River, 2 mi NE of Lesterville, Reynolds Co., Missouri, on State Road 21, by Perry C. and Virgie F. Holt, 22 Aug 1961.

*Distribution.*—Known only from the type locality.



275

*P. simondsi*

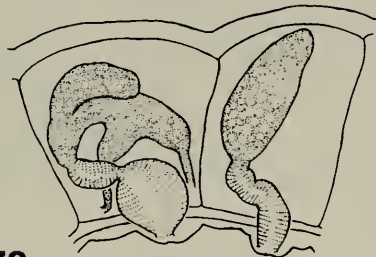


276



277

*S. attenuatus*



278



279

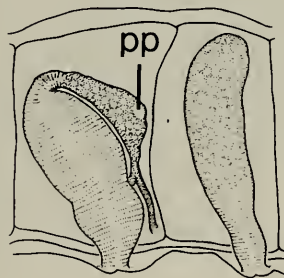


280



281

*S. carolinensis*



282



283

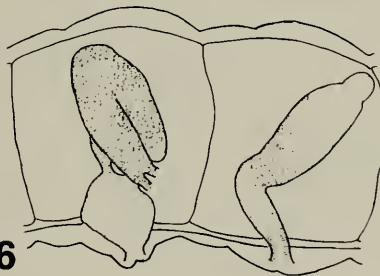


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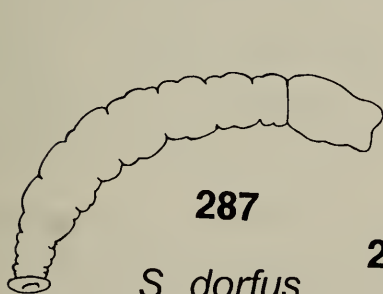


285

*S. chehalisae*



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287

*S. dorfus*



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289

290

Figs. 275–290. 275–276, *Pterodrilus simondsi* Holt; 277–280, *Sathodrilus attenuatus* Holt; 281–284, *Sathodrilus carolinensis* Holt; 285–286, *Sathodrilus chehalisae* Holt; 287–290, *Sathodrilus dorfus* Holt.

*Sathodrilus norbyi* Holt, 1977

Figs. 315–318

*Sathodrilus norbyi* Holt, 1977:125–128.

*Types.*—Holotype and 3 paratypes, USNM 53642, 15 paratypes, PCH 920, on *Pacifastacus leniusculus klamathensis* (Stimpson), from Union Flat Creek, ca. 13 km W of Pullman, Whitman Co., Washington, by Darwin E. Norby, 11 Jul 1958.

*Distribution.*—Idaho and Washington (Holt, 1977:127).

*Sathodrilus okaloosae* Holt, 1973

Figs. 319–325

*Sathodrilus okaloosae* Holt, 1973a:99–102.

*Types.*—Holotype, USNM 49715, 5 paratypes, USNM 49716, 2 paratypes, PCH 2720, on *Procambarus evermanni* (Faxon) and *P. versutus* (Hagen), collected 1.0 mi E of Santa Rosa Co. line on U.S. Highway 90, Okaloosa Co., Florida, by Horton H. Hobbs, III, 12 Aug 1968.

*Distribution.*—Known only from the type locality.

*Sathodrilus prostates* Holt, 1973

Figs. 326–331

*Sathodrilus prostates* Holt, 1973b:33–36.

*Types.*—Holotype, USNM 4532 [sic] (should be 45431), on *Procambarus acutus cuevachicae* (Hobbs), from El Ajenjibre, Mesa de San Diego, km 262 de la carretera México [Tuspan, Puebla, México], by A. Villalobos and H. H. Hobbs, Jr., 12 Apr 1957; 2 paratypes, USNM 45432, on the freshwater crab *Pseudohelphusa veracruzana*, from Rio Tapalapa, Veracruz, México, by A. Villalobos and H. H. Hobbs, Jr.; 1 paratype in the IBUM from the latter locality; 7 paratypes, PCH 700, from the latter locality.

*Distribution.*—From the lower slopes of the Sierra Oriental in Puebla to the lowlands of Veracruz, México.

*Sathodrilus rivigeae* Holt, 1988

Figs. 332–335

*Sathodrilus rivigeae* Holt, 1988b:804–807.

*Types.*—Holotype, USNM 119545, 2 paratypes, USNM 119546 (PCH 1089), on *Orconectes palmeri longimanus* (Faxon), from cool pools in a medium sized stream in Ouachita National Forest 3.2 mi E of Joplin, Montgomery Co., Arkansas, at crossing of U.S. Highway 270, by Perry C. and Virgie F. Holt, 23 Jun 1960.

*Distribution.*—Known only from the type locality.

*Sathodrilus shastae* Holt, 1981b

Figs. 336–338

*Sathodrilus shastae* Holt, 1981b:856–859.

*Types.*—Holotype, USNM 65230, 4 paratypes, PCH 1818, on *Pacifastacus fortis* (Faxon), from the headwaters of Fall River, Thousand Springs Ranch, Shasta Co., California, by Perry C. and Virgie F. Holt, 19 Aug 1964.

*Distribution.*—Known only from the type locality.

*Sathodrilus veracruzicus* Holt, 1968

Figs. 339–344

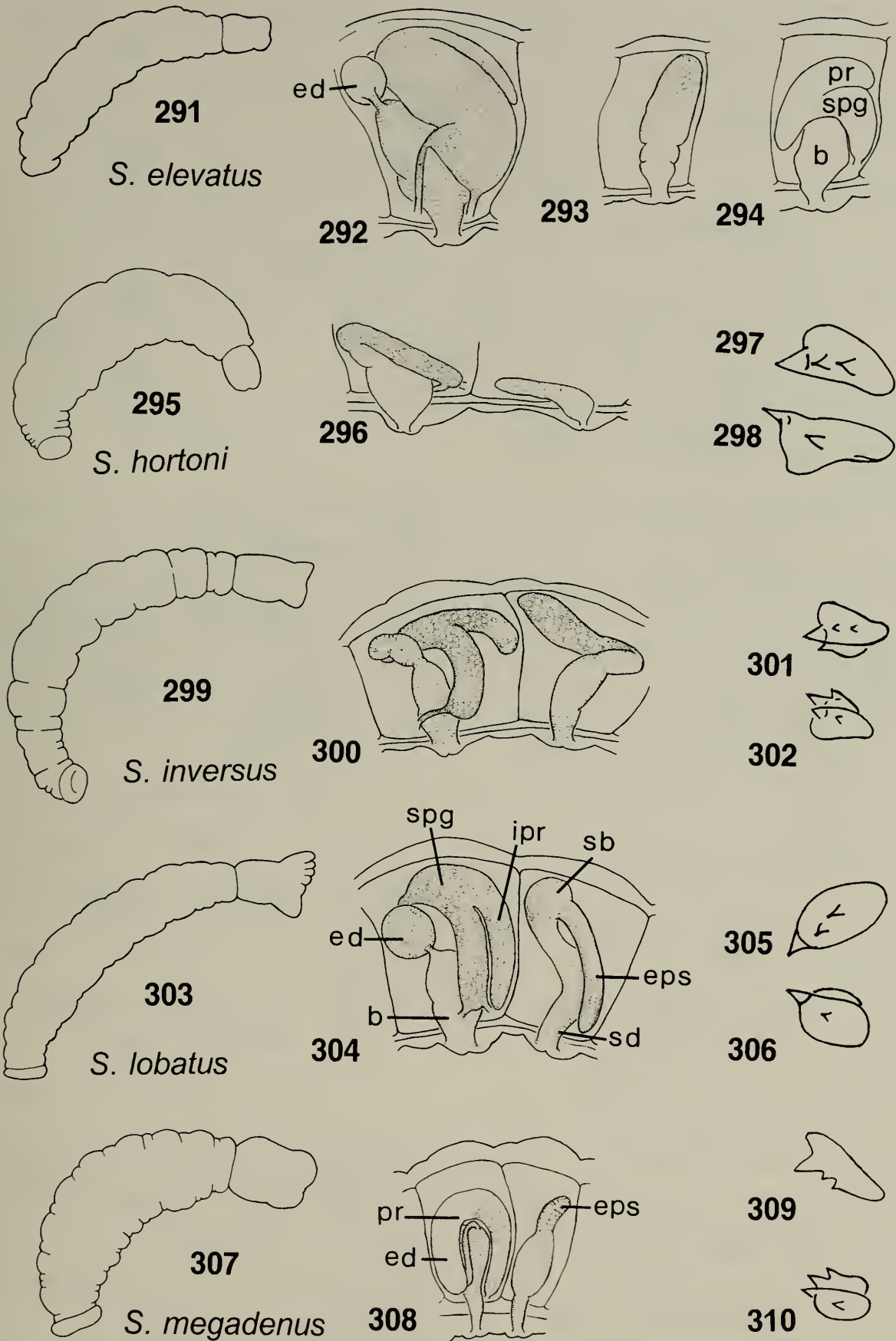
*Sathodrilus veracruzicus* Holt, 1968b:305–308.

*Types.*—Holotype, USNM 37105, 3 paratypes, USNM 37106, 3 paratypes, PCH 1623, on *Procambarus hoffmanni* (Villalobos), from waters near Coyutla, Veracruz, by Alejandro Villalobos, 16 Apr 1949.

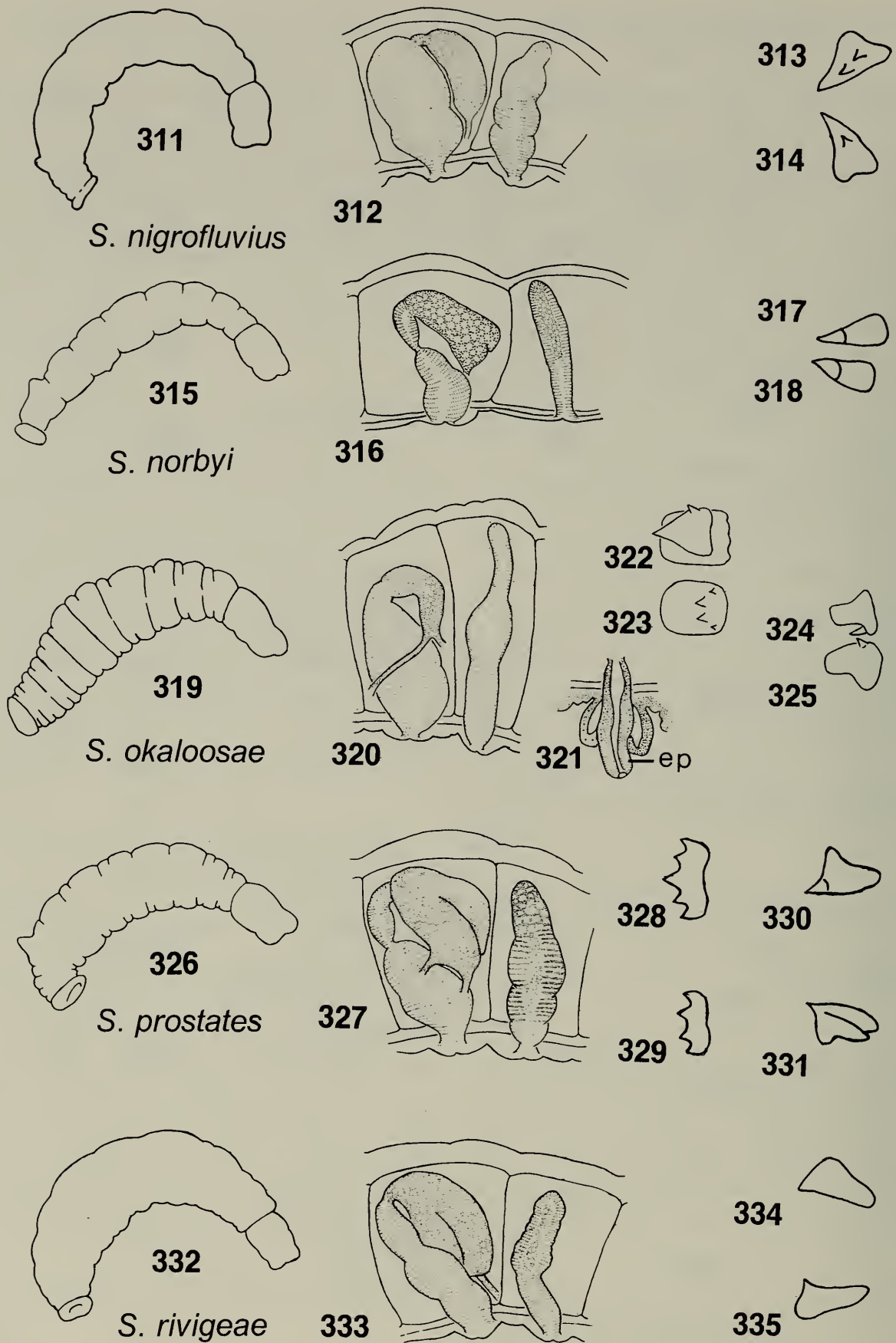
*Distribution.*—Known only from the type locality.

Notes: In the description of this species Holt (1968b:299, 307) correctly states that oral papillae are absent. In the description of *S. veracruzicus* it is incorrectly stated that oral papillae are present in both species. They are present only in *S. villalobosi*.





Figs. 291-310. 291-294, *Sathodrilus elevatus* (Goodnight), 292, left lateral view of reproductive system, 293, spermatheca, 294, right lateral view of reproductive system; 295-298, *Sathodrilus hortonii* Holt; 299-302, *Sathodrilus inversus* (Ellis); 303-306, *Sathodrilus lobatus* Holt; 307-310, *Sathodrilus megadenus* Holt.



Figs. 311-335. 311-314, *Sathodrilus nigrofluvius* Holt; 315-318, *Sathodrilus norbyi* Holt; 319-325, *Sathodrilus okaloosae* Holt, 321, lateral view of everted penis; 326-331, *Sathodrilus prostates* Holt; 332-335, *Sathodrilus rivigeae* Holt.

*Sathodrilus villalobosi* Holt, 1968

Figs. 345–348

*Sathodrilus villalobosi* Holt, 1968b:299–302, 1973b:36–38.

*Types.* — Holotype, USNM 37101, 4 paratypes, USNM 37102, 4 paratypes, PCH 208, on *Procambarus paradoxus* (Ortmann), from Tetela de Ocampo, Puebla, México, by Alejandro Villalobos, May 1941.

*Distribution.* — The type locality and Aqua Fria, Puebla, México.

*Sathodrilus wardinus* Holt, 1981

Figs. 349–352

*Sathodrilus wardinus* Holt, 1981b:859–861.

*Types.* — Holotype and 1 paratype, USNM 65229, 5 paratypes, PCH 921, on *Pacifastacus leniusculus klamathensis* (Stimpson), from Purdy Creek, 6 mi N of Gig Harbor, Pierce Co., Washington, by Darwin E. Norby, 26 Jun 1939.

*Distribution.* — Pierce Co., Washington.

*Tettodrilus* Holt, 1968

*Tettodrilus* Holt, 1968b:312.

*Type species.* — *Tettodrilus friaufi* Holt, 1968, by original designation.

*Gender.* — Masculine.

*Tettodrilus friaufi* Holt, 1968

Figs. 353–357

*Tettodrilus friaufi* Holt, 1968b:314–317.

*Types.* — Holotype, USNM 37099, 1 paratype, USNM 37100, on *Orconectes mirus* (Ortmann), *O. rhoadesi* Hobbs, *Cambarus graysoni* Faxon, and *C. tenebrosus* Hay, from a small stream ca. 8.5 mi S of Lewisburg, Marshall Co., Tennessee, on U.S. Highway 431, by Perry C. and Virgie F. Holt, 18 Apr 1960; 1 paratype, PCH 1007, on *C. graysoni* and *C. tenebrosus*, from a stream tributary to the Harpeth River, 2.4 mi S of Franklin, Williamson Co., Tennes-

see, on U.S. Highway 432, by Perry C. and Virgie F. Holt, 18 Apr 1960; 1 paratype, PCH 1008, on *C. graysoni*, from a small stream, 5.3 mi S of Franklin, Williamson Co., Tennessee, by Perry C. and Virgie F. Holt, 18 Apr 1960.

*Distribution.* — Streams of the Nashville Basin in middle Tennessee.

*Triannulata* Goodnight, 1940

*Triannulata* Goodnight, 1940:56.

*Type species.* — *Triannulata magna* Goodnight, 1940, by original designation.

*Gender.* — Feminine.

*Triannulata magna* Goodnight, 1940

Figs. 358–361

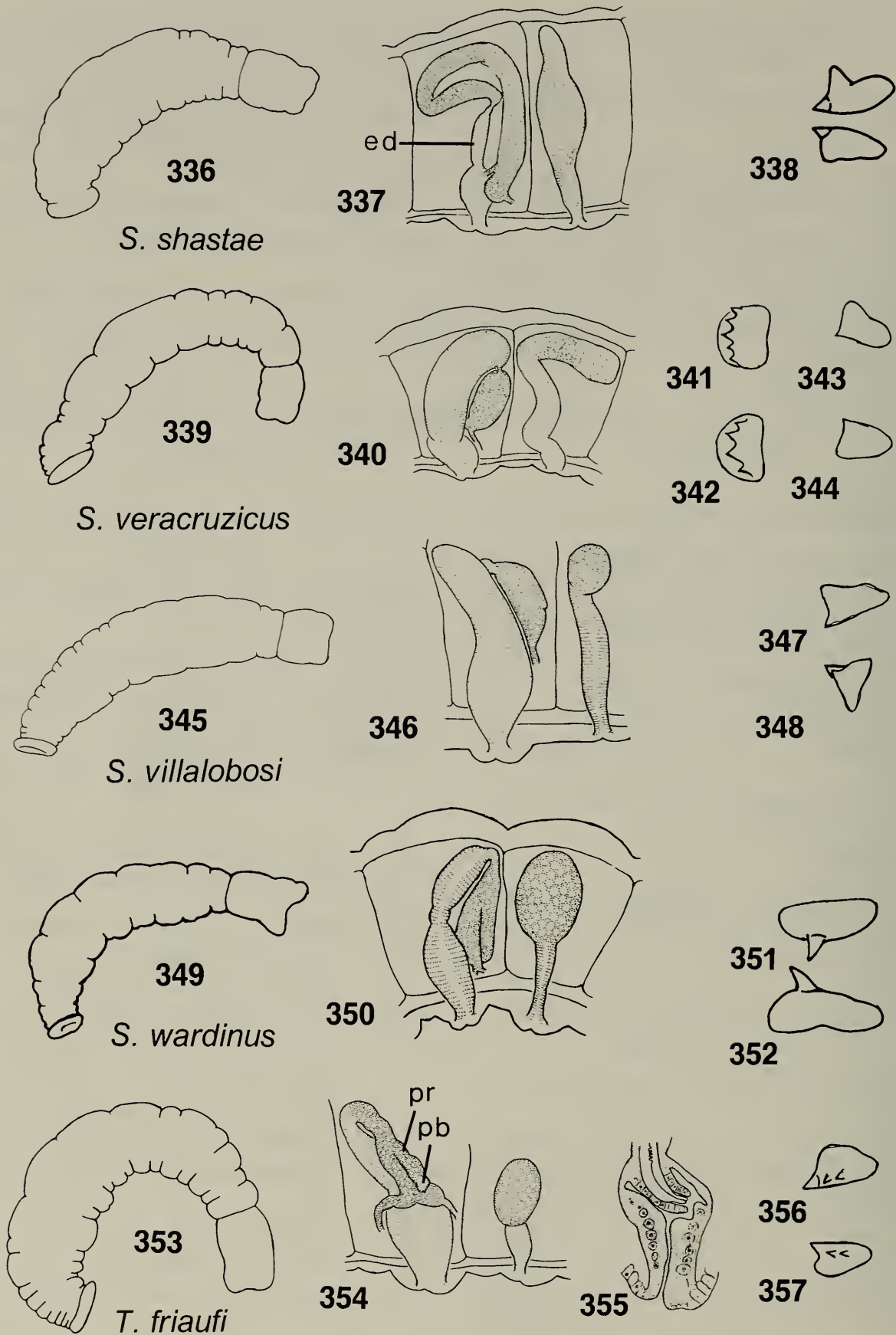
*Triannulata magna* Goodnight, 1940:56–57.—Holt, 1974:63–66.

*Types.* — Holotype, USNM 20567, on *Pacifastacus* sp., from Naches, Washington [collector and date unknown].

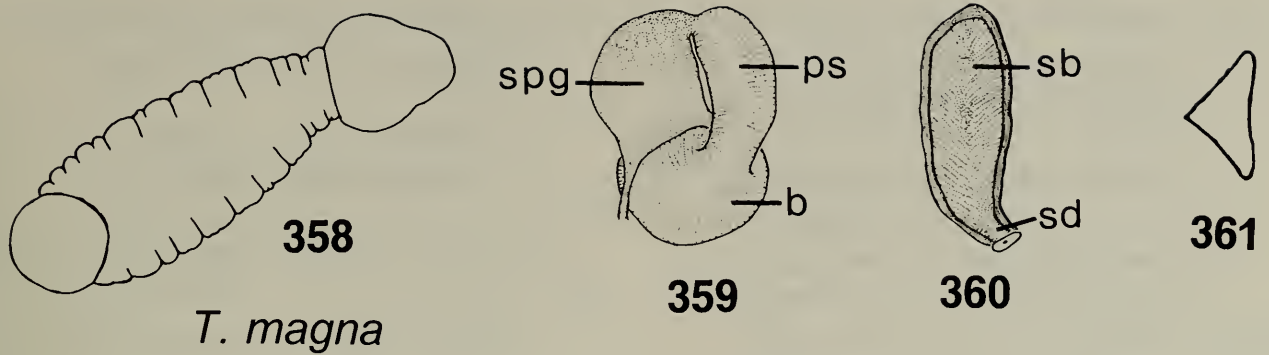
*Distribution.* — Yakima and Cowlitz Counties, Washington (Holt 1974:66).

Key to the Genera of Cambarincolidae (modified from Pennak, 1978)

- 1. Penis a protrusible muscular cone (Fig. 1B–E) . . . . . 2
- Penis eversible (Fig. 1F–I) . . . . . 4
- 2(1). Spermatheca absent; bursa asymmetrical and rounded (Figs. 225, 229) . . . . . *Ellisodrilus*
- Spermatheca present (Fig. 3) . . . . . 3
- 3(2). Length 2.5 mm or greater; no dorsal appendages present (Fig. 2) . . . . . *Cambarincola*
- Length less than 2.0 mm; cylindrical or fan-shaped dorsal appendages usually present on dorsal ridges (Figs. 253, 255) . . . . . *Pterodrilus*
- 4(1). Penis a cuticular tube, often very long (Fig. 1F–I) . . . . . *Oedipodrilus*



Figs. 336-357. 336-338, *Sathodrilus shastae* Holt; 339-344, *Sathodrilus veracruzicus* Holt; 345-348, *Sathodrilus villalobosi* Holt; 349-352, *Sathodrilus wardinus* Holt; 353-357, *Tettodrilus friaufi* Holt, 355, lateral view of bursa and penis.



Figs. 358–361. *Triannulata magna* Goodnight, 361, ventral view of upper jaw.

- |  |   |
|--|---|
| <ul style="list-style-type: none"> <li>– Penis with internal strands (Fig. 321) or an epithelial or muscular wall (Fig. 355) . . . . . 5</li> <li>5(4). Body segments II to VIII with cylindrical projections on dorsal surface (Fig. 218), upper lip with four tentacles . <i>Ceratodrilus</i></li> <li>– Without projections on body or tentacles on lip . . . . . 6</li> <li>6(5). Penis and ejaculatory duct a continuous, muscular eversible tube (Fig. 359) . . <i>Triannulata</i></li> <li>– Penis and ejaculatory duct distinct regions, ejaculatory duct not eversible (Figs. 350, 354) . . . . . 7</li> <li>7(6). Bursal atrium much longer than penial sheath; penial sheath eversible (Fig. 236) . . . . . <i>Magmatodrilus</i></li> <li>– Bursal atrium shorter than penial sheath; penial sheath not eversible (Fig. 278) . . . . . 8</li> <li>8(7). Semiducal gland small and slender, length and diameter about equal to that of ejaculatory duct (Fig. 354) . . . <i>Tettodrilus</i></li> <li>– Semiducal gland larger than ejaculatory duct (Fig. 278) . . . . . <i>Sathodrilus</i></li> </ul> | <ul style="list-style-type: none"> <li>2(1). Prostomial tentacles present (Fig. 112); spermathecal bulb cylindrical (Fig. 113) . . . . . <i>C. macrocephala</i></li> <li>– Prostomial tentacles absent (Fig. 178); spermathecal bulb oval (Fig. 179) . . . . . <i>C. restans</i></li> <li>3(1). Prostomial tentacles present (Figs. 49, 88) . . . . . 4</li> <li>– Prostomial tentacles absent (Fig. 2) . . . . . 8</li> <li>4(3). Spermathecal bulb with cylindrical ental process; semiducal gland with two lobes (Fig. 89) . . . . . <i>C. holti</i></li> <li>– Spermathecal bulb without ental process; semiducal gland without lobes (Fig. 50) . . . . . 5</li> <li>5(4). Body without prominent dorsal ridges (Fig. 94); prostate longer than semiducal gland (Figs. 95, 151) . . . . . 6</li> <li>– Body with prominent dorsal ridges (Fig. 49); prostate shorter than semiducal gland (Figs. 50, 173) . . . . . 7</li> <li>6(5). Prostomial tentacles small (Fig. 94); diameter of prostate less than that of semiducal gland (Fig. 95) . . . . . <i>C. ingens</i></li> <li>– Prostomial tentacles large (Fig. 150); diameter of prostate greater than that of semiducal gland (Fig. 151) . . . . . <i>C. montanus</i></li> </ul> |
|--|---|
- Key to the Species of *Cambarincola*
- |   |
|---|
| <ul style="list-style-type: none"> <li>1. Cephalic area conspicuously enlarged (Figs. 112, 178) . . . . . 2</li> <li>– Cephalic area of normal size (Fig. 2) . . . . . 3</li> </ul> |
|---|

- |         |   |         |   |
|---------|---|---------|---|
| 7(5).   | Prostomial tentacles large (Fig. 49); diameter of prostate three times that of seminiducal gland (Fig. 50) . . . . . <i>C. fallax</i>         | 14(13). | Seminiducal gland abruptly bent and U-shaped (Figs. 12, 14) . . . . . 15  |
| -       | Prostomial tentacles small (Fig. 172); diameter of prostate two times that of seminiducal gland (Fig. 173) . . . . . <i>C. philadelphicus</i> | -       | Seminiducal gland not U-shaped (Figs. 16, 20) . . . . . 19  |
| 8(3).   | Length of prostate greater than that of seminiducal gland (Figs. 78, 145) . . . . . 9   | 15(14). | Diameter of spermathecal bulb and duct similar (Figs. 44, 62) 16  |
| -       | Length of prostate equal to or less than that of seminiducal gland (Figs. 7, 99) . . . . . 11   | -       | Diameter of spermathecal bulb greater than that of duct (Fig. 12) . . . . . 17  |
| 9(8).   | Length of spermathecal bulb three times that of duct (Fig. 169); lower jaw with four teeth (Fig. 171) . . . . . <i>C. pamela</i>              | 16(15). | Spermatheca oval; length of prostate about half body diameter (Fig. 44) . . . . . <i>C. ellisi</i>                    |
| -       | Length of spermathecal bulb about 1.5 times that of duct (Fig. 78); lower jaw with two teeth (Fig. 80) . . . . . 10                           | -       | Spermatheca spherical; length of prostate one-fourth that of body diameter (Fig. 62) . . . . . <i>C. goodnighti</i>   |
| 10(9).  | Spermathecal bulb oval, diameter two times that of duct (Fig. 78) . . . . . <i>C. hoffmani</i>  | 17(15). | Length of spermathecal duct three times that of bulb (Fig. 12) . . . . . <i>C. barbarae</i>                           |
| -       | Spermathecal bulb lobed, diameter 1.5 times that of duct (Fig. 145) . . . . . <i>C. micradenus</i>  | -       | Length of spermathecal duct about 1.3 times that of bulb (Fig. 205) . . . . . 18                                      |
| 11(8).  | Length of prostate no more than one-third that of seminiducal gland (Figs. 72, 191) . . . . . 12  | 18(17). | Spermathecal bulb nearly spherical; length of prostate 1.5 times that of bursa (Fig. 205) . . . . . <i>C. susanae</i> |
| -       | Length of prostate at least half that of seminiducal gland (Figs. 12, 16) . . . . . 13  | -       | Spermathecal bulb elongate; length of prostate twice that of bursa (Fig. 217) . . . . . <i>C. vitreus</i>             |
| 12(11). | Seminiducal gland not bilobed; spermathecal duct longer than bulb (Fig. 72) . . . . . <i>C. heterognathus</i>                                 | 19(14). | Diameter of seminiducal gland 1.5 times that of prostate (Fig. 193) . . . . . <i>C. smalleyi</i>                      |
| -       | Seminiducal gland bilobed; spermathecal duct shorter than bulb (Fig. 191) . . . . . <i>C. shoshone</i>  | -       | Diameter of seminiducal gland at least twice that of prostate (Figs. 16, 20) . . . . . 20                             |
| 13(11). | Length of prostate about half that of seminiducal gland (Figs. 11, 16) . . . . . 14   | 20(19). | Seminiducal gland with two lobes (Figs. 20, 213) . . . . . 21   |
| -       | Length of prostate at least two-thirds that of seminiducal gland (Figs. 7, 99) . . . . . 25   | -       | Seminiducal gland not bilobed (Fig. 16) . . . . . 22  |
|         |   | 21(20). | Length of spermatheca about one-half body diameter (Fig. 20) . . . . . <i>C. branchiophilus</i>                       |
|         |   | -       | Length of spermatheca nearly as great as body diameter (Fig. 213) . . . . . <i>C. virginicus</i>                      |

|   |                         |         |   |                         |
|---|-------------------------|---------|---|-------------------------|
| 22(20). Length of bursa greater than that of seminiducal gland (Fig. 36) . . . . .  | <i>C. demissus</i>      | -       | four times that of duct (Fig. 105) . . . . .  | <i>C. leoni</i>         |
| - Length of bursa less than that of seminiducal gland (Figs. 16, 24) . . . . .  |                         |         | Diameter of spermathecal bulb 1.5 times that of duct (Fig. 108)   | 31                      |
| 23(22). Spermathecal bulb spherical (Fig. 16) . . . . .   | <i>C. bobbi</i>         | 31(30). | Length of spermatheca half that of body diameter; length of prostate two-thirds that of seminiducal gland (Fig. 108)              |                         |
| - Spermathecal bulb elongate (Figs. 24, 68) . . . . .   |                         |         | . . . . .   | <i>C. leptadenus</i>    |
| 24(23). Diameter of ejaculatory duct one-fifth that of bursa; diameter of prostate one-fourth that of seminiducal gland (Fig. 24) . . . . . | <i>C. carcinophilus</i> | -       | Length of spermatheca nearly equal to body diameter; length of prostate equal to that of seminiducal gland (Fig. 136)             |                         |
| - Diameter of ejaculatory duct one-half that of bursa; diameter of prostate one-half that of seminiducal gland (Fig. 68) . . . . .          | <i>C. gracilis</i>      | 32(27). | Diameter of spermathecal bulb at least twice that of duct (Figs. 38, 56) . . . . .  | 33                      |
| 25(13). Seminiducal gland bilobed (Figs. 3, 167) . . . . .  |                         | -       | Diameter of spermathecal bulb no more than 1.5 times that of duct (Figs. 7, 84) . . . . .   | 39                      |
| - Seminiducal gland not bilobed (Figs. 7, 30) . . . . .   |                         | 33(32). | Length of prostate equal to that of seminiducal gland (Figs. 56, 91) . . . . .  | 34                      |
| 26(25). Prostate and bursa of similar length (Fig. 3) . . . . .   | <i>C. acudentatus</i>   | -       | Length of prostate two-thirds that of seminiducal gland (Figs. 38, 130) . . . . .   | 36                      |
| - Length of prostate three times that of bursa (Fig. 167) . . . . .   | <i>C. ouachita</i>      | 34(33). | Lengths of prostate and bursa equal (Fig. 91) . . . . .   | <i>C. illinoisensis</i> |
| 27(25). Diameter of seminiducal gland equal to that of prostate (Fig. 105) . . . . .  |                         | -       | Prostate twice as long as bursa (Figs. 56, 161) . . . . .   | 35                      |
| - Diameter of seminiducal gland at least 1.5 times that of prostate (Figs. 7, 30, 84) . . . . .   |                         | 35(34). | Prostate straight; diameter of spermathecal bulb four times that of duct (Fig. 56); lower jaw with four teeth (Fig. 58) . . . . . | <i>C. floridanus</i>    |
| 28(27). Spermathecal bulb smaller than bursa (Fig. 124) . . . . .   | <i>C. manni</i>         | -       | Prostate J-shaped; diameter of spermathecal bulb 1.5 times that of duct (Fig. 161); lower jaw with two teeth (Fig. 163)           |                         |
| - Spermathecal bulb equal to or larger than bursa (Figs. 105, 108) . . . . .  |                         |         | . . . . .   | <i>C. olmecus</i>       |
| 29(28). Spermathecal duct about twice as long as spermathecal bulb (Fig. 197) . . . . .   | <i>C. speocirolanae</i> | 36(33). | Spermathecal bulb with a small ental lobe (Fig. 139) . . . . .  | <i>C. meyeri</i>        |
| - Spermathecal bulb longer than spermathecal duct (Fig. 105)  |                         | -       | Spermathecal bulb without an ental lobe (Fig. 38) . . . . .   | 37                      |
| 30(29). Diameter of spermathecal bulb   |                         | 37(36). | Seminiducal gland L-shaped (Fig. 38) . . . . .  | <i>C. dubius</i>        |

- Seminiducal gland oval or cylindrical (Figs. 130, 210) . . . . 38
- 38(37). Spermathecal bulb oval, diameter 3 times that of duct; prostate longer than bursa (Fig. 130) . . . . . *C. marthae*
- Spermathecal bulb spherical, diameter four times that of duct; lengths of prostate and bursa similar (Fig. 201) . . . . . *C. steevesi*
- 39(32). Prominent dorsal ridges present (Figs. 29, 180) . . . . . 40
- Dorsal ridges absent (Figs. 6, 83) . . . . . 41
- 40(39). Bursa longer than prostate; spermathecal duct and bulb equal in length (Fig. 30) . . . . . *C. chirocephala*
- Bursa shorter than prostate; spermathecal duct half as long as bulb (Fig. 181) . . . . *C. serratus*
- 41(39). Length of seminiducal gland less than that of bursa; spermathecal bulb with a large ental lobe (Fig. 7) . . . . . *C. alienus*
- Length of seminiducal gland equal to or greater than bursa; spermathecal bulb without large ental lobe (Figs. 84, 99) 42
- 42(39). Seminiducal gland L- or U-shaped (Figs. 165, 209) . . 43
- Seminiducal gland straight or slightly curved (Figs. 84, 99) 45
- 43(42). Bursa cylindrical, length twice its diameter (Fig. 118) . . . . . *C. macrodontus*
- Bursa oval, length no greater than 1.5 times its diameter (Figs. 165, 209) . . . . . 44
- 44(43). Seminiducal gland U-shaped; diameter of spermathecal duct less than that of prostate (Fig. 165) . . . . . *C. osceolai*
- Seminiducal gland L-shaped; diameter of spermathecal duct similar to that of prostate (Fig. 209) . . . . . *C. toltecus*
- 45(42). Upper and lower jaws with three teeth (Figs. 85, 86); spermathecal bulb cylindrical (Fig. 84) . . . . . *C. holostoma*
- Upper jaw with five teeth (Figs. 100, 156), lower with four or five teeth (Fig. 157); spermathecal bulb oval (Figs. 99, 155) 46
- 46(45). Lower jaw with one large and four small teeth (Fig. 187); length of prostate 1.5 times that of bursa (Fig. 185); body length 2.5 mm . . . . . *C. sheltensis*
- Lower jaw with four teeth of equal size (Figs. 101, 157); length of prostate and bursa similar (Fig. 99); body length less than 2.0 mm . . . . . 47
- 47(46). Length of prostate 0.8 times that of seminiducal gland; length of ejaculatory duct twice its diameter (Fig. 99); central tooth of upper jaw larger than lateral teeth (Fig. 100) . . . . . *C. jamapaensis*
- Length of prostate 0.6 times that of seminiducal gland; length and diameter of prostate equal (Fig. 155); teeth of upper jaw similar in size (Fig. 156) . . . . . *C. nanognathus*
- Key to the Species of *Ceratodrilus*
1. Length of tentacles on head 200  $\mu\text{m}$  (Fig. 218); projections on segments II–VII 146  $\mu\text{m}$  long . . . . . *C. ophiorhysis*
- Length of tentacles on head 90  $\mu\text{m}$  (Fig. 222); projections on segments II–VII 50  $\mu\text{m}$  long . . . . . *C. thysanosomus*
- Key to the Species of *Ellisodrilus*
1. Bursa large and bent, length about two-thirds body diameter (Fig. 229) . . . . . *E. clitellatus*
- Bursa not bent, length about



- half body diameter (Figs. 225, 233) ..... 2
- 2(1). Bursa wider than long; prostate diameter equal to that of seminiducal gland (Fig. 225) ..... *E. carronamus*
- Width and length of bursa about equal; diameter of prostate half that of seminiducal gland (Fig. 233) ..... *E. durbini*

Key to the Species of *Oedipodrilus*

- 1. Prominent dorsal ridges present ..... *O. oedipus*
- No dorsal ridges present .... 2
- 2(1). Spermathecal bulb and duct slender, diameters equal; spermathecal bulb bent at right angle to duct (Fig. 244) ..... *O. cuetzalanae*
- Spermathecal bulb and duct robust (Figs. 240, 248) ..... 3
- 3(2). Length of spermathecal duct half that of bulb; bursa straight (Fig. 240) ..... *O. anisognathus*
- Length of spermathecal duct 1.5 times that of bulb; bursa long and bent (Fig. 248) .... *O. macbaini*

Key to the Species of *Pterodrilus*

- 1. Four of five pairs of dorsal, fan-like projections on body (Fig. 253) ..... 2
- Body with one to seven pairs of dorsal, finger-like projections (Figs. 255, 263) ..... 3
- 2(1). Diameter of spermathecal bulb 1.5 times that of duct; diameter of seminiducal gland equal to that of bursa (Fig. 254) ... *P. alcicornus*
- Diameter of spermathecal bulb three times that of duct; diameter of seminiducal gland half that of bursa (Fig. 276) . *P. simondsi*

- 3(1). Length of prostate equal to that of seminiducal gland (Figs. 256, 260) ..... 4
- Length of prostate 0.6 to 0.5 times that of seminiducal gland (Figs. 264, 274) ..... 7
- 4(3). Diameter of bursa twice that of seminiducal gland; length of bursa half that of body diameter (Fig. 272) .... *P. mexicanus*
- Diameter of bursa one to 1.5 times that of seminiducal gland; length of bursa one-third or less that of body diameter (Figs. 256, 260) ..... 5
- 5(4). Length of spermathecal duct twice that of bulb (Fig. 256) . *P. cedrus*
- Length of spermathecal duct less than that of bulb (Fig. 260) ..... 6
- 6(5). Diameter of spermathecal bulb and duct equal; length of seminiducal gland and bursa equal (Fig. 260) ..... *P. choritonamus*
- Diameter of spermathecal bulb three times that of duct; length of seminiducal gland twice that of bursa (Fig. 268) .... *P. hobbsi*
- 7(3). Finger-like projections on the dorsal surface of seven body segments (Fig. 263); length of bursa about one-fourth that of body diameter (Fig. 264) .... *P. distichus*
- Finger-like projections on the dorsal surface of only one body segment (Fig. 273); length of bursa about half that of body diameter (Fig. 274) ..... *P. missouriensis*

Key to the Species of *Sathodrilus*

- 1. Tentacles on dorsal lips (Fig. 303) ..... *S. lobatus*
- Dorsal lips without tentacles (Fig. 277) ..... 2
- 2(1). Ejaculatory duct spherical, di-

- |   |                       |         |   |                        |
|---|-----------------------|---------|---|------------------------|
| ameter about half that of bursa (Fig. 292) . . . . .  | <i>S. elevatus</i>    | 11(10). | Length of spermathecal bulb four times that of duct (Fig. 327) . . . . .  | <i>S. prostates</i>    |
| - Ejaculatory duct cylindrical, diameter less than half that of bursa (Fig. 278) . . . . .                  | 3                     | -       | Lengths of spermathecal bulb and duct equal (Fig. 333) . . . . .  | <i>S. rivigeae</i>     |
| 3(2). Spermathecal bulb spherical or oval (Figs. 346, 350) . . . . .  | 4                     | 12(5).  | Seminiducal gland slender and looped, length greater than body diameter (Fig. 337) . . . . .  | <i>S. shastae</i>      |
| - Spermathecal bulb cylindrical (Figs. 278, 288) . . . . .  | 5                     | -       | Seminiducal gland short, length less than half body diameter (Figs. 282, 316) . . . . .   | 13                     |
| 4(3). Length of spermathecal duct four times the diameter of the bulb; prostate absent (Fig. 346) . . . . . | <i>S. villalobosi</i> | 13(12). | Diameter of seminiducal gland equal to that of bursa (Fig. 316) . . . . .   | <i>S. norbyi</i>       |
| - Length of spermathecal duct 1.3 times the diameter of the bulb; prostate present (Fig. 350) . . . . .     | <i>S. wardinus</i>    | -       | Diameter of seminiducal gland no more than 0.6 that of bursa (Figs. 312, 320) . . . . .   | 14                     |
| 5(3). Prostate present (Fig. 278) . . . . .   | 6                     | 14(13). | Length of seminiducal gland greater than that of bursa; length of spermatheca less than half body diameter (Fig. 296) . . . . .                       | <i>S. hortoni</i>      |
| - Prostate absent (Fig. 282) . . . . .  | 12                    | -       | Length of spermathecal gland less than that of bursa; length of spermatheca nearly equal to or greater than body diameter (Figs. 282, 312) . . . . .  | 15                     |
| 6(5). Length of spermathecal duct three times that of bulb (Fig. 288) . . . . .                             | <i>S. dorfus</i>      | 15(14). | Spermatheca bent, length 1.5 times body diameter (Fig. 340) . . . . .   | <i>S. veracruzicus</i> |
| - Length of spermathecal bulb equal to or greater than that of duct (Figs. 278, 308) . . . . .              | 7                     | -       | Spermatheca not bent, length equal to body diameter (Fig. 282) . . . . .  | 16                     |
| 7(6). Ejaculatory duct long, diameter equal to that of bursa (Fig. 308) . . . . .                           | <i>S. megadenus</i>   | 16(15). | Spermathecal bulb with a slender ental lobe whose length is equal to that of the spermathecal duct (Fig. 320) . . . . .                               | <i>S. okaloosae</i>    |
| - Ejaculatory duct short, diameter less than half that of bursa (Fig. 278) . . . . .                        | 8                     | -       | Spermathecal bulb without a long ental lobe (Figs. 282, 312) . . . . .  | 17                     |
| 8(7). Length of prostate about half that of seminiducal gland (Fig. 278) . . . . .                          | 9                     | 17(16). | Diameter of seminiducal gland about one-third that of bursa; spermathecal duct cylindrical; spermathecal bulb without ental lobe (Fig. 282) . . . . . | <i>S. carolinensis</i> |
| - Lengths of prostate and seminiducal gland equal (Fig. 286) . . . . .                                      | 10                    |         |   |                        |
| 9(8). Bursa spherical, length about one-third body diameter (Fig. 278) . . . . .                            | <i>S. attenuatus</i>  |         |   |                        |
| - Bursa cylindrical, length about half body diameter (Fig. 300) . . . . .                                   | <i>S. inversus</i>    |         |   |                        |
| 10(8). Length and width of bursa equal (Fig. 286) . . . . .   | <i>S. chehalisae</i>  |         |   |                        |
| - Length of bursa two to three times its width (Figs. 327, 333) . . . . .                                   | 11                    |         |   |                        |

- Diameter of seminiducal gland half that of bursa; spermathecal duct constricted; spermathecal bulb with short ental lobe (Fig. 312) . . . . *S. nigrofluvius*

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